

Revision of the Ethmolaimidae (Nematoda: Chromadorida)



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Synopsis

Based on the proposed synapomorphic character of preloacal supplementary copulatory organs of a unique derived form, the family Ethmolaimidae now contains both the Ethmolaiminae of Filipjev & Stekhoven, 1941 and the Neotonchinae of Wieser & Hopper, 1966. A tentative cladogram is proposed to express a theory of the relationships within the family. Several other taxonomic changes are proposed, including the erection of four new genera and six new species. Figures and keys are provided to facilitate species identification.

Introduction

The work reported here, prompted by the discovery of further new species from Scotland and Ireland, began as a review of just those species contained in Wieser & Hopper's (1966) subfamily Neotonchinae (raised to family by Lorenzen, 1981). However, similarities between these organisms and species of the genus *Ethmolaimus* (Ethmolaimidae) and a species of *Spiliphera* suggested that the respective taxa should be united. This paper sets out the arguments for this new combination of taxa, although the main descriptive work concentrates on the marine neotonchids.

In attempting to establish a sensible pattern of relationships among the ethmolaimids as a whole, cladistic methodology has been adopted in the belief that the concepts involved offer some hope of elucidating a coherent pattern in such a notoriously complicated group as the Nematoda. In this way, an attempt has been made to avoid providing taxonomic definitions based on a 'mélange of primitive characters' (Rosen, Forey, Gardiner & Patterson, 1981), where many features appear to be included unnecessarily. It should also be pointed out that although a theory of relationships is presented here in terms of a branching diagram, no claim is made that this necessarily reflects the evolutionary history of the organisms concerned.

Materials and methods

Ethmolaimid specimens studied are those contained in the descriptive section of this paper. The outgroup material specifically examined in order to determine the status of various characters is listed below.

Chromadoridae

Spilipherinae

Spiliphera gracilicauda De Man BMNH: 1980.4.20-21

Chromadorinae

Atrochromadora microlaima (De Man) BMNH: 1980.7.24-25

Prochromadora oerleyi (De Man) BMNH: 1958.12.5.20-27

Prochromadorella septimpapillata Platt BMNH: 1971.547

Euchromadorinae

Graphonema scampae (Coles) BMNH: 1963.616-17

Rhyps paraornata Platt & Zhang BMNH: 1981.4.19-21

Hypodontolaiminae

Dichromadora cephalata (Steiner) BMNH: 1980.7.23

Dichromadora hyalocheile (De Coninck & Stekhoven) BMNH: 1980.7.22

Hypodontolaimus balticus (Schneider) BMNH: 1980.5.76

Hypodontolaimus inaequalis (Bastian) BMNH: 1981.12.103

Neochromadora poecilosoma (De Man) BMNH: 1981.12.100-101

Cyatholaimidae

Pomponematinae

Pomponema reductum Warwick BMNH: 1968.274

Pomponema sedecima Platt BMNH: 1971.550

Pomponema tautraense (Allgen) BMNH: 1981.12.114

Paracanthonchinae

Paracyatholaimus sp. BMNH: 1980.7.1

Cyatholaiminae

Marylynnia complexa (Warwick) BMNH: 1980.6.49

Praeacanthonchus punctatus (Bastian) BMNH: 1981.12.104

Selachinematidae

Gammanema sp. BMNH: 1981.1.1

Synonchiella riemanni Warwick BMNH: 1980.6.51

Comesomatidae

Comesomatinae

Metacomesoma sp. BMNH: 1980.6.7

Sabatieriinae

Sabatieria breviseta Stekhoven BMNH: 1981.12.125

Sabatieria celtica Southern BMNH: 1981.12.124

Sabatieria pulchra (Schneider) BMNH: 1980.8.57

Dorylaimopsinae

Dorylaimopsis punctata Ditlevsen BMNH: 1980.6.26

Specimens were studied and photographed using microscopes fitted with interference contrast optics. Drawings, other than those taken from the literature, were made with a drawing tube.

The formula used in the description is a simplification of Filipjev's (1916) formula, itself a modification of Cobb's (1902) formula, where figures above the line indicate distance (in μm) from the anterior extremity to the posterior end of the oesophagus, vulva in females (or, in males and juveniles, and females where the vulva is not near the mid-point of the body, the letter 'M' designates the mid-point) and anus (cloaca in the male). Figures below the line represent corresponding body diameters at the head (conventionally taken at the level of the R_3 sensilla unless stated otherwise), base of oesophagus, mid-body and anus/cloaca. The total body length is placed after the line, followed by the De Man ratios 'a', 'b' and 'c' representing the ratio of total body length to maximum body diameter, oesophagus length and tail length respectively.

The following abbreviations are used: a.b.d. = anal/cloacal body diameter; c.d. = corresponding body diameter; h.d. = head diameter; R_1 , R_2 and R_3 sensilla refer to the inner labial, outer labial and cephalic sensilla respectively; S = spicule length; V = position of vulva from the anterior as a percentage of the total body length; L = total body length.

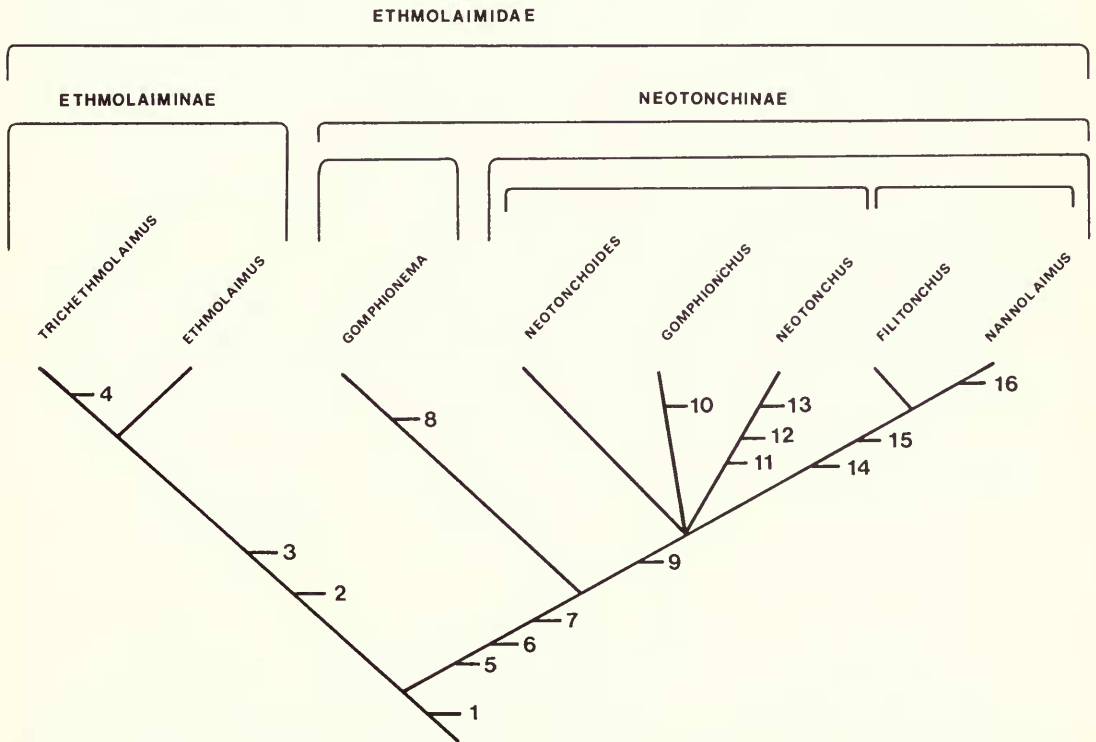


Fig. 1 Tentative cladogram expressing a theory of the relationships within the Ethmolaimidae. Numbered characters are those contained in the synapomorphy scheme in the text.

Synapomorphy scheme

At this stage the preferred theory of the interrelationships within the family Ethmolaimidae (as here defined) is introduced in order to facilitate discussion of the characters. The hypothesis is illustrated in Fig. 1. The following comparisons are based on the specimens contained in the descriptive section of this paper and the outgroups listed above.

- A. Ethmolaiminae has the following derived feature which it shares with the Neotonchinae:
1. Cup-shaped precloacal supplements with an external articulated flange.
- B. *Trichethmolaimus* also has the following features which it shares with *Ethmolaimus*:
2. Three large teeth, the subventral ones being as large or almost as large as the dorsal tooth.
 3. Amphid consists of one turn of the corpus gelatum.
- C. *Trichethmolaimus* has the following autapomorphic feature:
4. Extremely long somatic setae.
- D. *Gomphionema* has the character of A and also shares with the clade consisting of *Neotonchoides*, *Gomphionchus*, *Neotonchus*, *Filitonchus* and *Nannolaimus*:
5. Characteristically bent spicules.
 6. Dorso-sublateral subcephalic setae.
 7. Conical tail with rounded tip.
- E. *Gomphionema* also has the following autapomorphic feature:
8. Massive dorsal tooth only.
- F. Genera of the clade consisting of *Neotonchoides*, *Gomphionchus*, *Neotonchus*, *Filitonchus* and *Nannolaimus* have the characters of A and D and also have the following feature:
9. A patch of non-granulated cells in the vas deferens.
- No features could be detected which *Neotonchus*, *Gomphionchus* and *Neotonchoides* uniquely share and so the three genera constitute an unresolved trichotomy.
- G. *Gomphionchus* has the following autapomorphic feature:
10. Large anteriorly situated dorsal tooth.
- H. *Neotonchus* has the following autapomorphic features:
11. Sublateral pore-seta complexes.
 12. Lateral longitudinal row of caudal punctations.
 13. Characteristically shaped dorsal tooth.
- I. *Nannolaimus* has the characters of A, D and F and also shares with *Filitonchus*:
14. Elongate R_2 sensilla (equal to or longer than 1 h.d.).
 15. Loss of structurally expanded buccal lumen.
- J. *Nannolaimus* also has the following autapomorphic feature:
16. R_1 sensilla setiform.

Morphology and character evaluation

In discussing the taxonomically important morphological characters an attempt has been made to suggest at which taxonomic level of universality each feature is operating. This has necessitated making several crucial decisions, many of which may, in the light of future evidence, prove erroneous. However, the exigencies of cladistics do not allow these judgements to be avoided. In following the discussion, it may be helpful to refer to the tentative theory of relationships expressed in Fig. 1 and the species drawings in Figs 2–5.

Body shape. Most ethmolaimids are usually 600–1200 μm long with an 'a' ratio of around 30. However, species of *Nannolaimus* and *Filitonchus* tend to be slimmer animals, with an 'a' ratio of 50–100. The fixation-shape, the typical body shape when subjected to cold formalin fixation, is usually uncoiled. There is some anterior attenuation in most species, the head typically being about 60% of the width at the base of the oesophagus. The tail is conical except in *Ethmolaimus*, where it is conico-cylindrical.

Most of the features of overall body shape are not unique statements for ethmolaimids and therefore of little phylogenetic use. However, the shape of the tail appears to be useful at a high taxonomic level. Many other chromadorid groups have conical tails although in most, the tip is pointed, e.g. *Neochromadora poecilosoma*, *Hypodontolaimus inaequalis* and *Praeacanthonchus punctatus*. Other groups such as the Pomponematinae have characteristic conico-cylindrical tails with swollen tips. However, it is the rounded tail tip of the Neotonchinae which appears to be unique within the Chromadozoidea.

Cuticle ornamentation. The cuticle is annulated with each annule bearing one or more transverse rows of dots – the punctated cuticle – which are in fact cuticle supporting rods viewed end-on. In most species, the rods are short but in the head and tail regions of *Trichethmolaimus* they are elongated. These long rods are very similar in appearance to those found in *Pomponema* and other cyatholaimids.

There are many species in which the rows become irregular or fewer in number and also somewhat larger in the lateral field. Where there are fewer lateral rows, this is referred to as lateral differentiation: it is known to occur in eight of the 26 valid species but is not confined to particular genera. This lateral differentiation usually begins level with the base of the oesophagus, but in *Ethmolaimus pratensis* and *Gomphonema typicum* it starts just posterior to the amphid. The discontinuous distribution of the lateral differentiation and an apparently homologous occurrence in other chromadorid groups, e.g. Cyatholaimidae, suggests that it is the phenotypic expression of a symplesiomorphy. The alternative would be to assume that the condition had developed independently on many occasions, which seems less likely. In either case, the feature is phylogenetically irrelevant within the Ethmolaimidae.

In *Neotonchoides melotridus* studied here and as reported for *Neotonchus boucheri* by Boucher (1976), and for *Neotonchoides corcundus* and *Nannolaimus fusus* by Gerlach (1956), some species have certain complete rows consisting of larger dots. The presence of the character could not be verified in *Neotonchus boucheri* or *Nannolaimus fusus* specimens studied here. However, pending further information, its limited discontinuous distribution is probably best considered as representing analogous conditions.

In all four *Neotonchus* species there are lateral rows of irregular dots on the posterior third of the tail. This feature is considered synapomorphic for the genus since it was not detected in any of the other ethmolaimids nor in those specimens used as outgroup comparisons for the synapomorphy scheme.

Cuticle pores. Lateral and sublateral cuticle pores have been observed and documented many times (Sharma, Hopper & Webster, 1979). Cuticle pores were also observed in all the species studied with the exception of *Nannolaimus phaleratus*. The actual pattern of their distribution appears to vary among species and may be useful autapomorphic features characterising species, e.g. *Neotonchoides vitius*. However, there is no evidence that the pores in the Ethmolaimidae are different from those of other chromadorids or cyatholaimids, so their presence is considered phylogenetically irrelevant. In *Neotonchus* species, the sublateral pores posterior to the oesophagus each have a seta situated medially to them: called here pore-seta complexes. This combination appears to be a unique derived character, not detected in any other specimens studied.

Cephalic sensilla. Ethmolaimids have the plesiomorphic 6 + 6 + 4 cephalic sensilla arrangement (Lorenzen, 1981) so the character 'three circles of cephalic sensilla at different levels' is irrelevant. Only in groups such as the Cyatholaiminae, where the R_2 and R_3 sensilla are *always* at the same level, i.e. the relationship is stabilised, does this relationship become of phylogenetic significance. In the *Nannolaimus fusus* specimen studied, the sensilla were very close together although not exactly at the same level as depicted by Gerlach (1956). Within the Ethmolaimidae, there is a range in the degree of separation of the R_2 and R_3 sensilla, so the arrangement in *Nannolaimus fusus* can be considered convergent with that of the Cyatholaiminae. In most species, the R_3 sensilla are longer than the R_2 sensilla whilst the

R_1 sensilla are papilliform or not detectable. The R_1 sensilla are setiform in *Nannolaimus* species while in *N. fusus* the R_2 sensilla are longer than the R_3 sensilla. It will be argued below that the character 'setiform R_1 sensilla' is autapomorphic for the genus whilst the relative length of the two circles is probably irrelevant.

However, there is one character of the setation which does appear to be stabilised within a part of the Ethmolaimidae; the presence of a seta situated dorso-sublaterally just posterior to the level of the R_3 sensilla and often level with the amphid. The feature has been used to separate *Trichethmolaimus* and *Ethmolaimus* from the others (Fig. 1). In *Gomphionema* species, *Gomphionchus lutosus* and *Ethmolaimus pratensis*, the ventro-sublateral caudal setae appear to be particularly well developed and spine-like. The best interpretation is that the feature is not congruent since a clade containing these species requires a less parsimonious interpretation of other character states than that provided in Fig. 1.

Amphids. The amphids in all ethmolaimids are spiralled ventrally to the centre. Determining the exact number of 'turns' of the amphid is not easy: whereas the structure always appears to begin on the dorsal side, it is difficult to determine where the last turn ends. What is actually being observed, of course, is the wall of a spiralling groove in which lies the corpus gelatum. Following the course of the wall usually gives a count of one more than the turns of the corpus gelatum and is often reported as a count of 'n' plus a 'bit more'. Whether the 'bit more' is a $\frac{1}{4}$, $\frac{1}{2}$ or $\frac{3}{4}$ appears to vary among specimens even of the same species. However, the number of complete turns is a useful character at the species level. To simplify matters, in this work the amphids are described as 'n+', where 'n' is the number of complete turns of the wall. Most species have 3+ or 4+ amphids, although they may be up to 6+. In *Gomphionema*, both sexes have the same number of turns. However, in certain other genera where females are known, they have one less turn than the male. Unfortunately, most species are known from males only, so the extent of this sexual dimorphism and its phylogenetic importance remains unknown.

The amphids of *Trichethmolaimus* and *Ethmolaimus* have fewest turns of all, being apparently just one turn of the corpus gelatum (hence a possible wall count of 2+ turns), although the wall in *Ethmolaimus* may be only lightly cuticularised and therefore difficult to distinguish, particularly with normal light microscopy. Although essentially a multi-spiralled amphid, in these two genera, the number of turns, pending evidence to the contrary, is used here to characterise the subfamily to which these two genera will be consigned (Fig. 1). The apparently similar condition found in *Spiliphera* (Chromadoridae) must be considered homoplastic.

The widespread occurrence of multi-spiralled amphids among the outgroup comparisons and Chromadoria generally indicate that the character is plesiomorphic for the Ethmolaimidae. The amphid in the Ethmolaiminae may then possibly represent an example of reversal.

Buccal cavity. All species have the anterior part divided into twelve sections, a feature shared by all taxa within the suborder Chromadorina (Lorenzen, 1981). The degree of development of the dentition and the form of the buccal cavity posterior to the teeth are highly variable features and seem to show sufficient discontinuity to be of use in delimiting sets of genera (Fig. 1). The possession of a distinct dorsal tooth and a structurally expanded conical posterior part are characters found in all the chromadorid outgroups and so are judged to be plesiomorphic. If this is the case, the absence of an expanded buccal lumen in *Filitonchus* and *Nannolaimus* must be a derived feature, representing the terminal state of a transformation series in which the polarity is towards a reduction in cuticularisation, a simplification of the character.

Oesophagus. In all members of the Ethmolaimidae, the oesophagus ends in a muscular bulb. However, its degree of development is correlated with the size of the dorsal tooth, being poorly developed and difficult to detect in *Nannolaimus* and *Filitonchus* but large and conspicuous in *Gomphionema*, *Ethmolaimus* and *Trichethmolaimus*. The character

'oesophagus bulb present' is irrelevant phylogenetically within the Ethmolaimidae, being apparently homologous with the structures found in several other nematodes, e.g. Chromadoridae.

Copulatory structures. All ethmolaimids have paired spicules which in the known species are of equal size, mostly about the same length as the cloacal diameter. As pointed out by Wieser & Hopper (1966), in many species the shape viewed from a lateral perspective is rather characteristic, being bent about one-third of the distance from the distal end. This shape, typically as depicted in Figs 4a–c, appears to be unknown outside the set defined here as the subfamily Neotonchinae: it is not shared by species of *Trichethmolaimus* or *Ethmolaimus*. Those species within the Neotonchinae (on other grounds) which do not have this typical spicule shape are assumed, on grounds of parsimony, to display an autapomorphic condition.

The gubernaculum, as in most chromadoroid groups, is represented only by a lightly cuticularised rod-like structure, in lateral view, and is of no phylogenetic importance. However, lying lateral to the distal ends of the spicules in *Ethmolaimus*, *Gomphionema*, *Gomphionchus* and at least one species of *Neotonchoides*, there is an additional structure resembling a cone or triangular plate, possibly the cuticularised end of a duct. If homologous, the structure must be considered plesiomorphic since any group made up of those species in which the feature can be detected is not congruent with other characters. Well developed lateral pieces are also known in the Euchromadorinae.

All species studied here, and most of those described in the literature, possess a prominent ventral precloacal spine, a plesiomorphic character known to occur in other nematode groups, e.g. *Dichromadora* and *Pomponema* species.

Anterior to the precloacal spine in all ethmolaimid species there is a single ventral row of between 6 and 24 cup-shaped supplements occupying 7–30% of the total body length. Other chromadoroid groups have been described as having cup-shaped supplements, but in none of these other taxa do the supplements seem to be identical in detail. The 'cup' part of the supplement, when viewed laterally, is continuous, without the dorsal aperture seen in many other chromadoroid supplements, e.g. *Prochromadorella septempapillata*. The anterior and posterior ends of the 'cup' may be thickened, as in *Gomphionema*, but in many species the curve is the same thickness at all parts of the semi-circle. The external part of the cup is surrounded by a longitudinal oval flange with a pore in the middle (Fig. 30d). The anterior and posterior parts of this flange appear to be articulated, allowing the whole supplement to be protruded or retracted, and are particularly noticeable in *Ethmolaimus pratensis*, *Gomphionchus lutosus* and *Gomphionema fellator*.

The outgroup species investigated, in which the supplements are most similar to those of the ethmolaimids, were *Atrochromadora microlaima* which does not have external flanges and *Dichromadora cephalata* which does have external flanges. As far as can be ascertained, the supplements of *Dichromadora cephalata* are indistinguishable from those of certain ethmolaimids, e.g. *Neotonchoides vitius*. It may be that the flange is not articulated in *D. cephalata* but since it cannot be stated categorically that they are articulated in all ethmolaimid species this must remain only a possible difference. However, *Dichromadora* differs from the ethmolaimids on so many other grounds, e.g. cuticle ornamentation, amphid shape, number of testes and tail shape, that it must be concluded that the ethmolaimid supplement shape is the result of homoplasy in *D. cephalata*. Certainly, it is worth noting that within the Ethmolaimidae all species have the typical flanged supplement, whilst among the outgroups apparently similar structures occur only sporadically, even within a genus, cf. *Dichromadora cephalata* and *Dichromadora hyalocheile*. Therefore, it is suggested that the specific structure of the supplements is a crucial stable synapomorphic character indicating that the Ethmolaimidae is a monophyletic unit. Furthermore, the condition probably represents the terminal state of a transformation series in which polarity is determined by increasing complexity. The number of supplements may be of some use at the

species level since in all but *Ethmolaimus pratensis* and *Gomphonema typicum* the range of variation appears to be $n \pm 1$ ($n = \text{mode}$).

Reproductive system. All species have two opposed gonads. Females have both ovaries reflexed and of equal size. In the male, the testes are outstretched but the posterior one is smaller than the anterior in most species (Fig. 18f). The testes normally lie on opposite sides of the gut but there is no stability within genera as to whether the anterior gonad is to the left or right, although it is constant within species.

In at least eight of the species studied there appears to be a series of about five cells in the vas deferens which are of a non-granular appearance (Fig. 28d). They usually stand out as a distinct patch, generally located level with the fourth to sixth supplement from the cloaca. Within a species, not all specimens display the character, suggesting that it may be a feature appearing at a particular stage in development. However, when the feature is visible, it always occurs in the same place. Despite its discontinuous distribution, this character, here called simply the 'clear patch', has been used to delimit a set of genera within the Ethmolaimidae (Fig. 1). Nothing resembling this feature could be detected amongst the outgroups.

Ecology and distribution

Most ethmolaimids are found in marine sediments, particularly in fine sand, silt and muds with a relatively high organic content. They have been reported from intertidal locations down to 650 m and from the North Atlantic, the Mediterranean, Australia and South America. In most ecological investigations they seem to represent only a small proportion of the total nematode fauna. For example, in a recent study only 32 specimens of a species of *Neotonchoides* were found among 13,645 nematodes and so did not appear in tables of the most abundant species (Platt, 1977). However, in a study of Australian beach nematodes, a species of *Gomphonema* was one of the dominant species (Warwick, pers. comm.). It therefore seems that in keeping with our knowledge of most marine nematodes, we have yet to discover the preferred habitat of most ethmolaimid species. A practical consequence of this lack of knowledge is that most species descriptions are of necessity based on only a few specimens.

Unlike most of the genera, *Ethmolaimus* is found in freshwater and brackish habitats, which perhaps accounts for its failure in the past to be linked with some of those entities which are here considered to belong to the same group.

Taxonomic revision

In the following diagnoses, taxa above the family level are assumed to have the characters proposed as synapomorphies by Lorenzen (1981), namely:

Chromadorina: vestibule of buccal cavity divided into twelve parts.

Chromadoroidea: punctated cuticle.

Family ETHMOLAIMIDAE Filipjev & Stekhoven, 1941

Neotonchidae Wieser & Hopper, 1966 syn. nov.

TYPE GENUS. *Ethmolaimus* De Man, 1880

DIAGNOSIS. Chromadoroidea. Ventral row of conspicuous cup-shaped supplements, each with an external articulated flange. Amphid multi-spiralled. Two testes.

REMARKS. The subfamilies Ethmolaiminae and Neotonchinae were raised to family level by Lorenzen (1981) but in doing so he was unable to distinguish any synapomorphies and was therefore obliged to resort to a characteristic combination of primitive characters. None of

these characters was a unique statement for the respective groups and monophyly was not established. Gerlach & Riemann (1973) had earlier placed the genera *Ethmolaimus* and *Spiliphera* in the same subfamily within the Chromadoridae. However, as discussed above, an examination of the supplements of *Ethmolaimus* and *Spiliphera hirsuta* (= *Trichethmolaimus*) suggests that they have a derived structure compared with those of the Chromadoridae. Therefore it is proposed that the group consisting of *Ethmolaimus*, *Trichethmolaimus* and the genera of the Neotonchinae be considered a monophyletic family, for which the senior synonym Ethmolaimidae is available.

Lorenzen (1981) refrained from establishing forms with a multi-spiralled amphids as a monophyletic group since he wanted to transfer the Comesomatidae to the order Monhysterida on the grounds of their ovaries being outstretched rather than reflexed. This somewhat controversial move assigns taxonomic supremacy to the reproductive system and has the consequence of requiring the condition 'spiral amphids and punctated cuticle' to have arisen independently on more than one occasion. Despite some reservations, for the purposes of this discussion Lorenzen's argument is accepted but the multi-spiralled amphid is treated as a plesiomorphic character for the Chromadoroidea since they also occur in the Desmodoroidea, e.g. *Eubostrichus*. The inclusion of multi-spiralled amphids in the diagnosis simply serves to draw attention to this unresolved problem.

Several species within the Ethmolaimidae have transverse rows of punctations which are discontinuous in the lateral field, a feature which appears to be homologous with that of certain members of the Cyatholaimidae and thus may constitute a synapomorphy linking the families, e.g. *Praeacanthonus punctatus*.

Subfamily ETHMOLAIMINAE Filipjev & Stekhoven, 1941

TYPE GENUS. *Ethmolaimus* De Man, 1880.

DIAGNOSIS. Ethmolaimidae. Three large teeth, the subventral teeth being as large or almost as large as the dorsal tooth. Amphid consisting of one turn of the corpus gelatum.

REMARKS. This subfamily contains the genera *Ethmolaimus* and *Trichethmolaimus*. In addition to the diagnostic features, the genera also share the following characters: buccal cavity posterior to the level of the teeth cylindrical and cuticularised; tail has a pointed tip.

ETHMOLAIMUS De Man, 1880

SYNONYMY. See Gerlach & Riemann, 1973.

TYPE SPECIES. *Ethmolaimus pratensis* De Man, 1880.

DIAGNOSIS. Ethmolaimidae. R₂ sensilla papilliform.

REMARKS. No derived characters uniquely shared by species of this genus could be found which would also separate it unequivocally from *Trichethmolaimus* other than the lack of long somatic setae. As currently constituted, the genera can be separated on the relative size of the R₂ sensilla, although this may not prove very satisfactory in the future. Other characters of *Ethmolaimus* species, but not necessarily exclusive to them, are: R₃ sensilla papilliform or short setae; short (about 3 a.b.d.) conico-cylindrical tail. In addition, the species studied here (*E. pratensis*) had the following features which may or may not be shared with other species: lateral differentiation; cuticle pores; lateral spicule piece; two testes.

In Hirshmann's (1952) revision of the genus, the diagnosis only consisted of primitive characters which left its systematic position in some doubt (Jensen, 1979a). However, based on the form of the supplements they can now be linked with the Neotonchinae.

There are three valid species: *E. pratensis* De Man, 1880; *E. multipapillosus* Paramonov, 1926; *E. dahli* Gerlach, 1953 (see Table 1).

E. distaphanus De Cillis, 1917 is a *nomen nudum* (Goodey, 1963); and *E. faeroensis*

Ditlevsen, 1928 and *E. caudatus* Alekseev, Naumova & Dymina, 1979, being based only on females, are here considered *species inquirenda*. *E. parapatensis* Alekseev, Naumova & Dymina, 1979 is morphometrically within the range of variation reported for *E. pratensis* by Hirshmann (1952); it has subventral teeth smaller than the dorsal tooth as reported for *E. pratensis* by Jensen (1979a) and appears to have supplements similar to those of *E. pratensis* described here. Therefore, the species should be synonymised.

TRICHETHMOLAIMUS gen. nov.

TYPE SPECIES. *Spiliphera hirsuta* Gerlach, 1956.

DIAGNOSIS. Ethmolaiminae. Extremely long somatic setae. Cuticle supporting rods elongated in head region. R_2 sensilla setiform and stout. Tail conical with pointed tip.

REMARKS. The species originally described as *Spiliphera hirsuta* by Gerlach (1956) from Kiel Bay differs from the other two valid species of *Spiliphera*, *S. dolichura* De Man, 1893 and *S. gracilicauda* De Man, 1893, in possessing two testes, lacking the characteristic pairs of sub-lateral setae level with the posterior end of the buccal cavity, having precloacal supplements and a short conical tail in addition to the long somatic setae. On these grounds, *S. hirsuta* has been removed from *Spiliphera*. In several respects the species is similar to *Ethmolaimus*, especially in buccal cavity structure. However, in view of the long somatic setae, elongated cuticle rods in the head region, setiform R_2 sensilla, conical tail and fully marine habitat, it seems there are sufficient differences to support the erection of a new genus, the only species becoming *Trichethmolaimus hirsutus* (Gerlach, 1956) (*lapsus hirsuta*).

Subfamily NEOTONCHINAE Wieser & Hopper, 1966

TYPE GENUS. *Neotonchus* Cobb, 1933.

DIAGNOSIS. Ethmolaimidae. Dorso-sublateral subcephalic setae. Spicules a characteristic shape, bent about one-third from the distal end. Conical tail with rounded tip.

REMARKS. This subfamily is the apomorphic sister group of the Ethmolaiminae (Fig. 1) and contains genera without large subventral teeth. All known neotonchids have an amphid consisting of more than one turn of the corpus gelatum (wall count of 3+ or more); a plesiomorphy, assuming the amphid found in the outgroups is homologous.

GOMPHIONEMA Wieser & Hopper, 1966

TYPE SPECIES: *Gomphionema typicum* Wieser & Hopper, 1966.

DIAGNOSIS. Neotonchinae. Massive dorsal tooth only. Large posterior oesophageal bulb. Spicule with lateral pieces. Tail in male with two or three stout ventro-sublateral spines. Supplements occupy about 30% of total body length.

REMARKS. The characters of the diagnosis, other than the size of the dorsal tooth, are not considered to be synapomorphies. Other features of the valid species, but not necessarily exclusive to them or shared by all, are: lateral differentiation; R_3 sensilla short; amphid 3+ turns in both sexes and situated well anterior; 14–24 supplements.

By including the proportion of the body length occupied by the supplements the intention is to draw attention to this as a possible differentiating feature. In other neotonchids with a large number of supplements, e.g. *Gomphionchus lutosus* and *Neotonchoides votadinii*, the proportion of the body occupied is less than in *Gomphionema* even when the number of supplements is the same. Perhaps it is the area to be occupied by supplements that is genetically programmed rather than the total number.

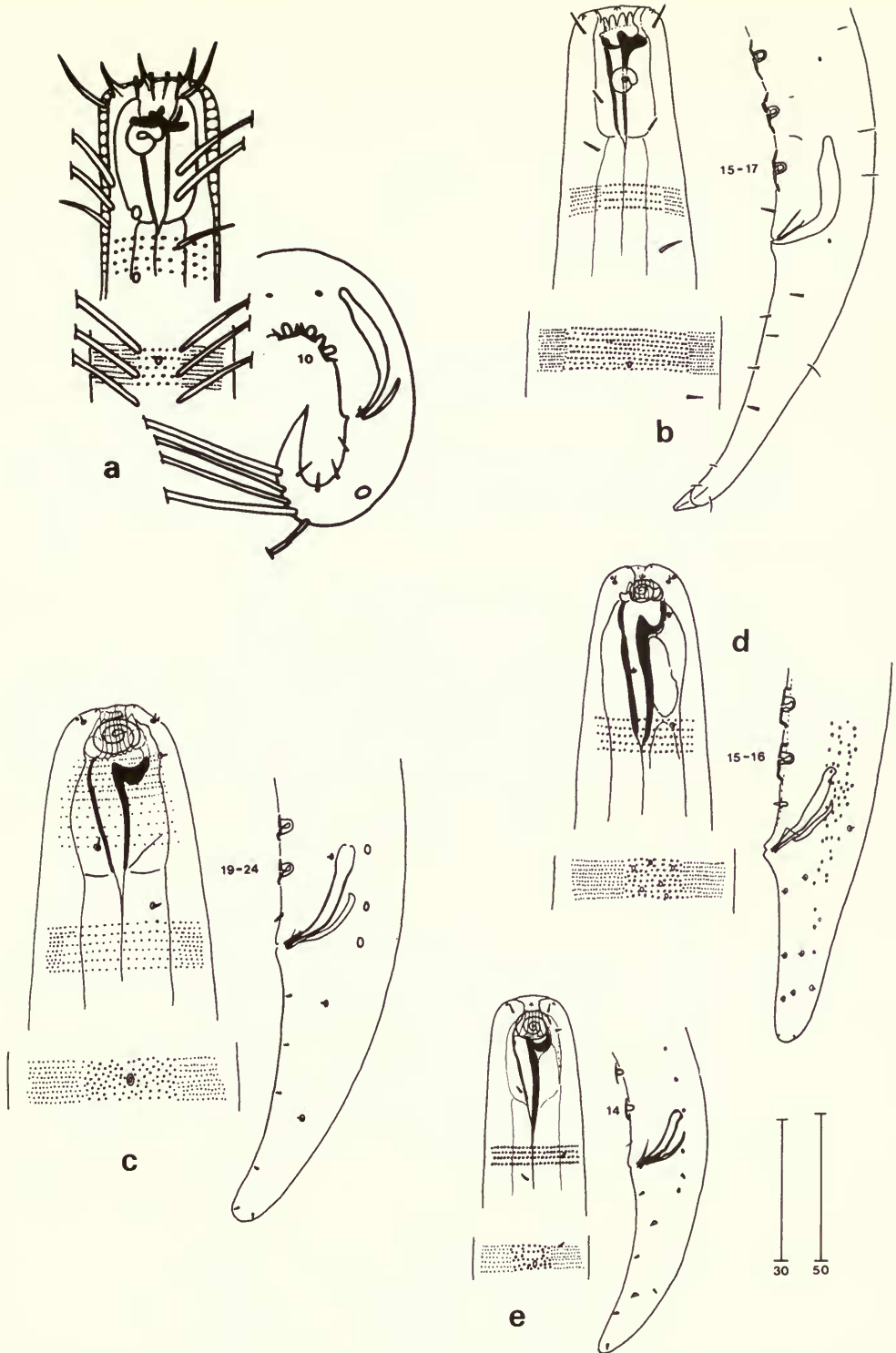


Fig. 2 (a) *Trichethmolaimus hirsutus*; (b) *Ethmolaimus pratensis*; (c) *Gomphionema typicum*; (d) *Gomphionema fellator*; (e) *Gomphionema* sp. Bar scales in microns; left bar for head, right bar for tail.

Table 1 Main differentiating data of *Ethmolaimus*, *Gomphonema* and *Gomphionchus* species (measurements in μm)

Species	L	a	b	c	R ₃	A σ	A φ	S	Ps	T	Distribution
<i>Ethmolaimus pratensis</i>	385-1200	13-35	4-8	5-14	7-8	2+	2+	40-43	9-17	l/r	Europe & USSR
<i>Ethmolaimus multipapillosus</i> *	830-1230	17-28	7-8	8-14	pap.	2+	2+	32	21-24	?	Europe
<i>Ethmolaimus dahli</i> *	710-775	19	5-6	9-13	pap.	2+	?	36	20-21	?	Chile
<i>Gomphonema typicum</i>	1240-1530	18-22	6-7	13-15	2	3+	3+	41-47	19-24	l/r	E. coast USA
<i>Gomphonema fellator</i>	645-1035	15-26	4-6	11-17	1	3+	3+	36-38	15-16	l/r	E. coast USA
<i>Gomphonema curipus</i>	920	26	6	13	5	3+	?	23	16	?	Suez Canal
<i>Gomphonema</i> sp.	835	22	6	12	2	3+	?	25	14	r/l	Australia
<i>Gomphionchus lutosus</i>	870-1020	21-24	8	12-14	3	4+	?	29	20	l/r	E. coast USA

Abbreviations: L = total body length; a, b and c = De Man ratios; R₃ = length of R₃ sensilla; A σ and A φ = number of turns of σ and φ amphid; S = absolute length of spicule; Ps = number of prelocaal supplements; T = disposition of testes relative to gut (l = left, r = right), anterior/posterior; pap. = papilliform sensilla. Data from own observations and/or published descriptions.

*Specimens not seen.

Gerlach (1957) described *G. compactum* (as *Neotonchus compactus*) from Brazil, based on a single juvenile female: this species is here considered dubious. Riemann & Rachor (1972) subsequently described a single male from the Suez Canal as *G. compacta*. However, the specimen cannot be Gerlach's *G. compacta* since it lacks lateral differentiation: it also lacks the cuticle pores found in other *Gomphonema* species. The Suez specimen therefore warrants recognition as a separate species, named *Gomphonema euripus* sp. nov. (*euripus* L=canal), the holotype being the specimen on which Riemann & Rachor's (1972) description was based.

Gomphonema now contains three valid named species, *G. typicum* Wieser & Hopper, 1966, *G. fellator* Wieser & Hopper, 1966 and *G. euripus* sp. nov. plus a new species from Australia to be described by Dr R. M. Warwick. These valid species may be distinguished by using the information in Table 1 and Fig. 2.

Clade: *NEOTONCHOIDES/GOMPHIONCHUS/NEOTONCHUS/
FILITONCHUS/NANNOLAIMUS*

These five genera, discussed below, all share the occurrence of a clear patch in the vas deferens. Together, they form the apomorphic sister group of *Gomphonema* and could be designated a tribe. However, it seems inappropriate at this stage to formalise taxonomically such groups since they are based on what must at best be considered only tentative information.

Clade: *NEOTONCHOIDES/GOMPHIONCHUS/NEOTONCHUS*

In these three genera there is a well-developed buccal cavity with a distinct dorsal tooth which, by comparison with outgroups, is taken to be a plesiomorphic feature. As remarked earlier, no synapomorphies could be found for these genera so they must remain an unresolved trichotomy separated from the clade consisting of *Filitonchus* and *Nannolaimus* by the absence of those features which characterise the latter.

NEOTONCHUS Cobb, 1933

Heterocyatholaimus Allgen, 1935 syn. nov.

TYPE SPECIES. *Neotonchus punctatus* Cobb, 1933.

DIAGNOSIS. Neotonchinae. Cuticle has sublateral pores each associated with a seta. Posterior third of tail with lateral row of small punctations. Buccal cavity wide with a characteristic triangular dorsal tooth and two small subventral teeth. Clear patch in vas deferens.

REMARKS. As here redefined, the genus contains only four valid species: *N. punctatus* Cobb, 1933; *N. chamberlaini* Wieser & Hopper, 1966; *N. boucheri* sp. nov. (syn. *N. chamberlaini sensu* Boucher, 1976 nec Wieser & Hopper, 1966); *N. meeki* Warwick, 1971. Jensen (pers. comm.) considered *Heterocyatholaimus* Allgen, 1935 congeneric with *Neotonchus* although the only species, *H. macrolaimus*, is so poorly described from a single female that it should be regarded as a dubious species. *N. hapalus* Vitiello, 1974 and *N. spiralis* Vitiello, 1974 are both *nomen nuda*.

In addition to the diagnostic features, valid species have the following characters: lateral differentiation (except *N. boucheri*); R₃ sensilla 30–35% h.d.; amphid 3+ to 5+ turns, 50–70% c.d. and at least in *N. boucheri* the female has one fewer turns than the male; 6–8 precloacal supplements. With the exception of *N. punctatus*, all species had a clear patch in the vas deferens. *N. punctatus* had a vas deferens in which there was an area of cells which had a different appearance from the rest of the vas deferens (Fig. 16). Since this was in a position where a clear patch might be expected, perhaps in freshly preserved specimens it would be the clear patch.

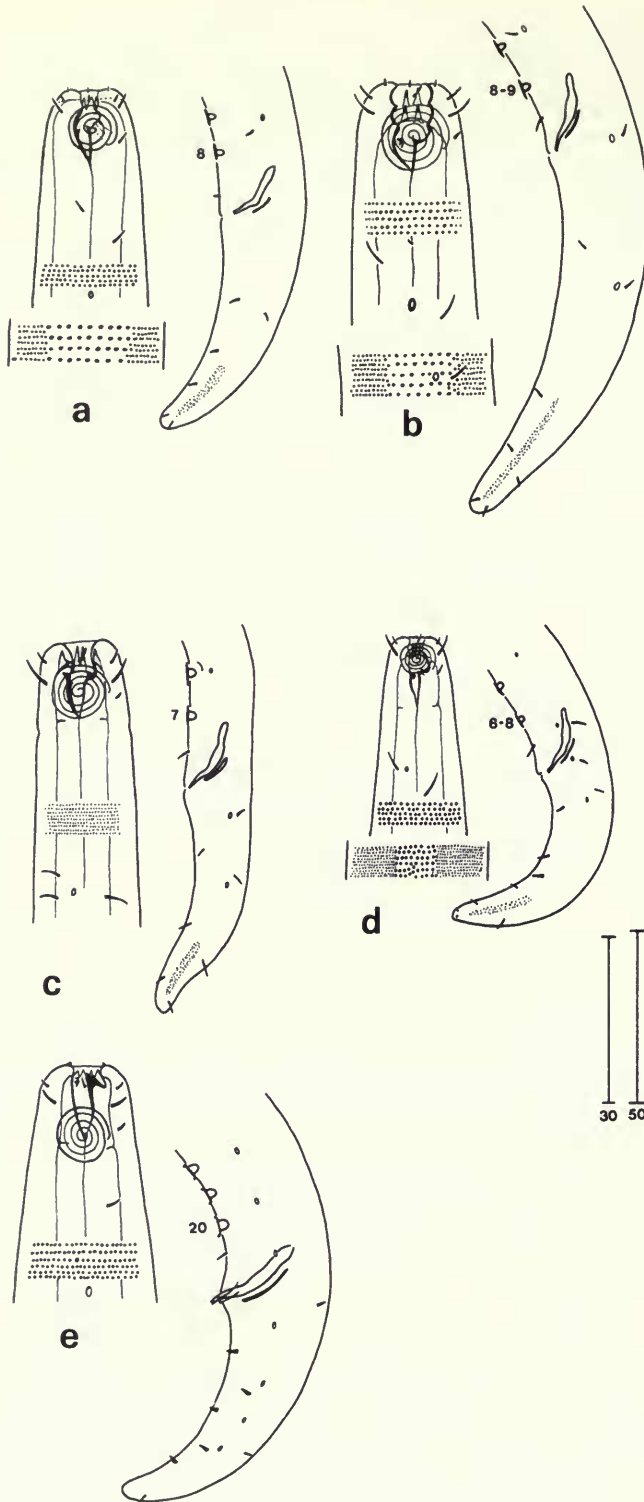


Fig. 3 (a) *Neotonchus punctatus*; (b) *Neotonchus chamberlaini*; (c) *Neotonchus boucheri*; (d) *Neotonchus meeki*; (e) *Gomphionchus lutosus*. Bar scales as in Fig. 2.

Table 2 Main differentiating data of *Neotonchus* species (measurements in μm)

Species	L	a	b	c	R ₂	R ₃	A σ	A ϕ	T	Cp	Ps	Location
<i>N. punctatus</i>	722	28	7	11	1.5	3	3+	?	r/r	-	8-9	E. coast USA
<i>N. chamberlaini</i>	960	29	7	8	4	6	5+	?	r/l	+	8-9	E. coast USA
<i>N. boucheri</i>	590-755	24-34	6-7	9-11	2-3	5-6	4+	3+	l/?	+	7	English Channel
<i>N. meeki</i>	710-750	25-29	6-7	9	2-3	6-7	4+	4+	l/r	+	6-8	North Sea

Abbreviations: R₂ = length of R₂ sensilla; Cp = presence (+) or absence (-) of clear patch in vas deferens; others as Table 1.

The shape of the dorsal tooth is rather characteristic but difficult to put into words. It is like an equilateral triangle projecting out from the wall of the buccal cavity and, compared with *Neotonchoides*, it is not forward-pointing (cf. Figs 3 a–d & 4 a–j).

The species may be distinguished using the information in Table 2 and Fig. 3.

GOMPHIONCHUS gen. nov.

TYPE SPECIES. *Neotonchus lutosus* Wieser & Hopper, 1966.

DIAGNOSIS. Neotonchinae. Large forward-pointing dorsal tooth situated anteriorly in the buccal cavity and protruding into the vestibule. Clear patch in vas deferens.

REMARKS. The form of the buccal cavity appears to be so different from the other neotonchids that a distinct genus is justified for *Neotonchus lutosus*. The buccal cavity form is the only autapomorphy which could be detected, the clear patch being synapomorphic. Other, non-exclusive, features are: lateral cuticle pores; amphid 4+ turns, situated posterior to R₃ sensilla; spicule with lateral pieces; male with ventro-sublateral caudal spines. Characters of use in identification are contained in Table 1 and Fig. 3e.

NEOTONCHOIDES gen. nov.

Comesa Gerlach, 1956 syn. nov.

TYPE SPECIES. *Neotonchoides cuanensis* sp. nov.

DIAGNOSIS. Neotonchinae. Buccal cavity with a distinct forward-pointing tooth and ventral ridges but no definite subventral teeth. Clear patch in vas deferens.

REMARKS. In 1956, Gerlach described a specimen from Kiel Bay as *Comesa corcunda* gen. et sp. nov. Wieser & Hopper (1966) noted the similarity between Gerlach's description and Cobb's specimens of *Neotonchus punctatus*, which they deemed congeneric. However, Gerlach's (1956) description gives no indication that *Comesa corcunda* fits the new definition of *Neotonchus* given above, so in the absence of specimens it is removed from *Neotonchus*. It would be possible to make Gerlach's species the type of a genus to hold all those taxa transferred from *Neotonchus*, which would then become *Comesa* species. But since the opportunity presents itself, it seems more sensible to base the genus on a species for which there is a good series of type specimens available. Such a species would be the one described here from Ireland, for which the new genus *Neotonchoides* is erected. Until specimens become available which might prove to the contrary, *Comesa corcunda* is transferred to the new genus.

Vitiello (1970) described a species as '*Neotonchus aff. corcundus*' which differed from Gerlach's (1956) species on the relative size of the spicule and its less heavily cuticularised buccal cavity, in addition to the other minor differences pointed out by Vitiello (1970). Vitiello's specimens warrant recognition as a separate species, which is named after him as *Neotonchoides vitielloii* sp. nov., the holotype being the male specimen on which Vitiello's (1970) description was based.

Warwick & Buchanan (1970) also recorded the presence of '*Neotonchus corcundus*' from the Northumberland coast. Examination of their material showed it to represent a distinct species new to science which is named *Neotonchoides warwicki* sp. nov. and described below.

The following species are considered valid: *N. melotridus* (Wieser & Hopper, 1966) comb. nov.; *N. corcundus* (Gerlach, 1956) comb. nov.; *N. vitius* (Warwick, 1971) comb. nov.; *N. interruptus* (Warwick, 1971) comb. nov.; *N. votadinii* (Warwick, 1971) comb. nov.; *N. pseudocorcundus* (Vitiello, 1971) comb. nov.; *N. cupulatus* (Vitiello, 1970) comb. nov.; *N. cuanensis* sp. nov.; *N. warwicki* sp. nov.; *N. vitielloii* sp. nov.

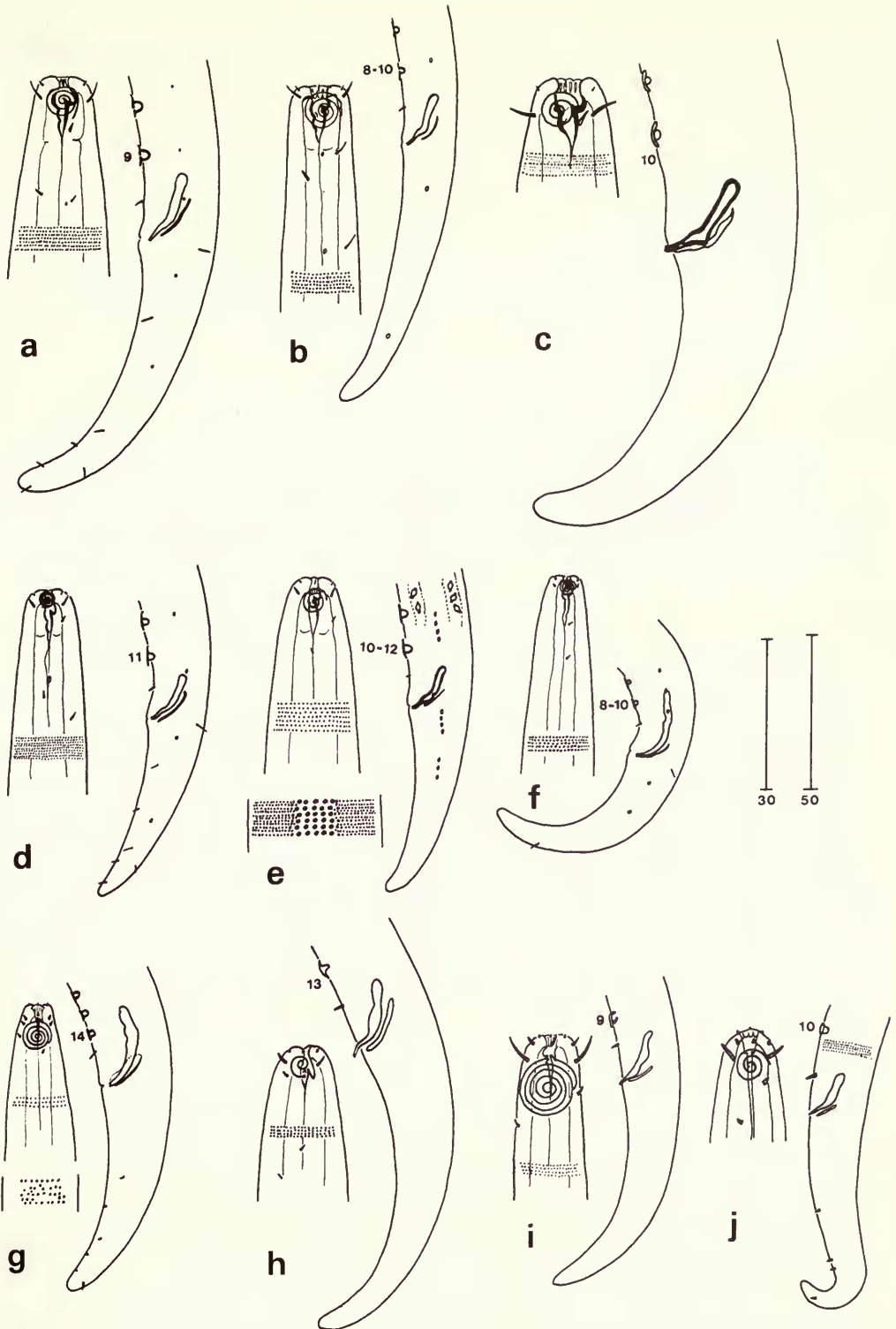


Fig. 4 (a) *Neotonchooides melotridus*; (b) *Neotonchooides cuanensis*; (c) *Neotonchooides corcundus* (after Gerlach, 1956); (d) *Neotonchooides warwicki*; (e) *Neotonchooides vitius*; (f) *Neotonchooides interruptus*; (g) *Neotonchooides votadinii* (after Warwick, 1971); (h) *Neotonchooides pseudocorcundus* (after Vitiello, 1971); (i) *Neotonchooides cupulatus* (after Vitiello, 1970); (j) *Neotonchooides vitielloii* (after Vitiello, 1970). Bar scales as in Fig. 2.

The proposed diagnostic feature for *Neotonchoides*, absence of definite subventral teeth, is admittedly a weak character but no positive autapomorphies could be found for the genus. In addition to the diagnostic characters, other features of the valid species, not necessarily shared by all, are: lack of lateral differentiation, except *N. vitius* and *N. votadinii*; R_3 sensilla 20–50% h.d., except *N. interruptus*; amphids 3+ or 4+ turns, except *N. cupulatus* with 5+ turns; amphid 30–70% c.d., except *N. cupulatus*; 8–14 preloacal supplements. In the only species in which females are known, *N. cuanensis*, the amphid of the female has one less turn than that of the male.

N. pseudocorcundus was described as having just over two turns of the amphid (Vitiello, 1971), but since the amphid is depicted as spiralling in the 'wrong' direction (Fig. 4h) one may assume that it was not clearly visible and a reinvestigation may show the species to have more turns of the amphid.

The species may be distinguished using the information in Table 3 and Fig. 4.

Clade: *FILITONCHUS/NANNOLAIMUS*

These two genera form the apomorphic sister group of *Neotonchoides/Gomphionchus/Neotonchus*. Synapomorphies are: buccal cavity not structurally expanded; R_2 sensilla elongate, one or more head diameters. Other characters currently displayed by the constituent species are: slender body, 'a' ratio about or greater than 50; long R_3 sensilla; dorsal tooth, if present, only a small peg; 4–6 amphid turns in male; no lateral differentiation of cuticle.

NANNOLAIMUS Cobb, 1920

TYPE SPECIES. *Nannolaimus guttatus* Cobb, 1920.

DIAGNOSIS. Neotonchinae. R_1 sensilla setiform. R_2 sensilla elongate. Buccal cavity not structurally expanded. Clear patch in vas deferens.

REMARKS. This genus is transferred from the Cyatholaimidae. According to Lorenzen (1981) the monophyly of the Cyatholaimidae is based on the R_2 and R_3 sensilla being at the same level. Whilst in the type and in *Nannolaimus fusus* described by Gerlach (1956) the two circles are close together, in the specimens of *N. fusus* studied here they were not at exactly the same level and there are grounds for questioning the setal arrangement in *N. guttatus* (see below). As discussed earlier, the setal arrangement in some *Nannolaimus* species is considered as convergent with the condition found in the Cyatholaimidae since the presence of typical supplements and a posterior oesophageal bulb, albeit weak, supports their position within the Ethmolaimidae. A connection between *Nannolaimus* and *Gomphionema* was also noted by Riemann & Rachor (1972).

N. guttatus Cobb, 1920 was described from a single female specimen and should be considered a *species inquirenda*. However, there are a number of interesting points contained in Cobb's description: he figures the cuticle as having lateral differentiation; the R_1 sensilla are very long and depicted in a position posterior to the lips, i.e. not where they normally occur, which suggests that the disposition of the cephalic setae may have been misinterpreted; the intestinal cells had granules with 'the appearance of hollow shells', a description which would fit the structures found in *Neotonchoides vitius* (see below).

Nannolaimus complicatus Gerlach, 1957 does not belong to this genus: the tail is conico-cylindrical; R_1 sensilla are not setiform; supplements are absent. The species shows more similarity with *Paralongicyatholaimus* Stekhoven, 1950 to which genus it is proposed to transfer it: *Paralongicyatholaimus complicatus* (Gerlach, 1957) comb. nov., syn. *Nannolaimus complicatus* Gerlach, 1957. *Nannolaimus volutus* Gerlach, 1956 is transferred to *Filitonchus*. *Nannolaimus labiosus* Vitiello, 1974 is a *nomen nudum*.

Neotonchus phaleratus Wieser & Hopper, 1966 has the characters of *Nannolaimus* as now defined and is transferred to this genus. The only two valid species therefore are *N. phaleratus* (Wieser & Hopper, 1966) comb. nov. and *N. fusus* Gerlach, 1956. In addition to

Table 3 Main differentiating data of *Neotonchooides* species (measurements in μm)

Species	L	a	b	c	R ₂	R ₃	A σ	A φ	Sp	Ps	T	Cp	Location
<i>N. melotridus</i>	1140	42	10	12	0.7	4	3+	?	0.9	9	l/r	-	E. coast USA
<i>N. cuanensis</i>	810-1115	37-64	8-10	9-16	2	4-5	4+	3+	0.9	8-10	l/r	-	Irish Sea
<i>N. corcundus</i> *	1280	28	7	12	1	7	3+	?	0.9	10	?	?	Baltic
<i>N. warwicki</i>	750-785	31-33	7-8	12-13	0.5	3	3+	?	0.9	11	r/l	+	North Sea
<i>N. vittius</i>	690-780	23-29	6-7	12	1	2	3+	?	0.9	10-12	l/r	+	North Sea
<i>N. interruptus</i>	630-680	30	7-8	10-11	1	1	3+	?	1.5	8-10	l/r	-	North Sea
<i>N. viodini</i> *	820	23-33	7	10-11	1.5	1.5	4+	?	0.9	14	?	?	North Sea
<i>N. pseudocorcondus</i> *	1115-1345	35-42	9-11	10-13	+	3	2+	?	0.9	13	?	?	Mediterranean
<i>N. cupulatus</i> *	745	35	8	11	2.6	6	5+	?	0.9	9	?	?	Mediterranean
<i>N. vittelloit</i> *	915	44	8	12	+	4.5	3+	?	0.5	10	?	?	Mediterranean

Abbreviations: Sp = approximate length of spicule as proportion of distance from cloaca to first precloacal supplement; others as Tables 1 & 2.
*Specimens not seen.

Table 4 Main differentiating data of *Nannolaimus* (*N.*) and *Filitonchus* (*F.*) species (measurements in μm)

Species	L	a	b	c	R ₂	R ₃	A σ	A φ	T	Cp	Ps	Location
<i>N. fuscus</i>	1245	66	9	11	11	6	6+	?	l/r	-	9-10	Irish Sea; Baltic
<i>N. phaleratus</i>	960-1000	51	8	9	9-10	12-14	4+	3+	l/l	+	8	E. coast USA
<i>N. filiformis</i>	1190-1300	86-99	12	16	5-6	9	4+	?	r/l	+	8-9	North Sea
<i>F. ewensis</i>	1370	81	13	14	6	8	6+	?	r/l	+	7	W. coast Scotland
<i>F. volutus</i> *	1555	48	7	10	15	15	5+	?	?	?	8	Baltic

Abbreviations: See Tables 1 & 2.
*Specimens not seen.

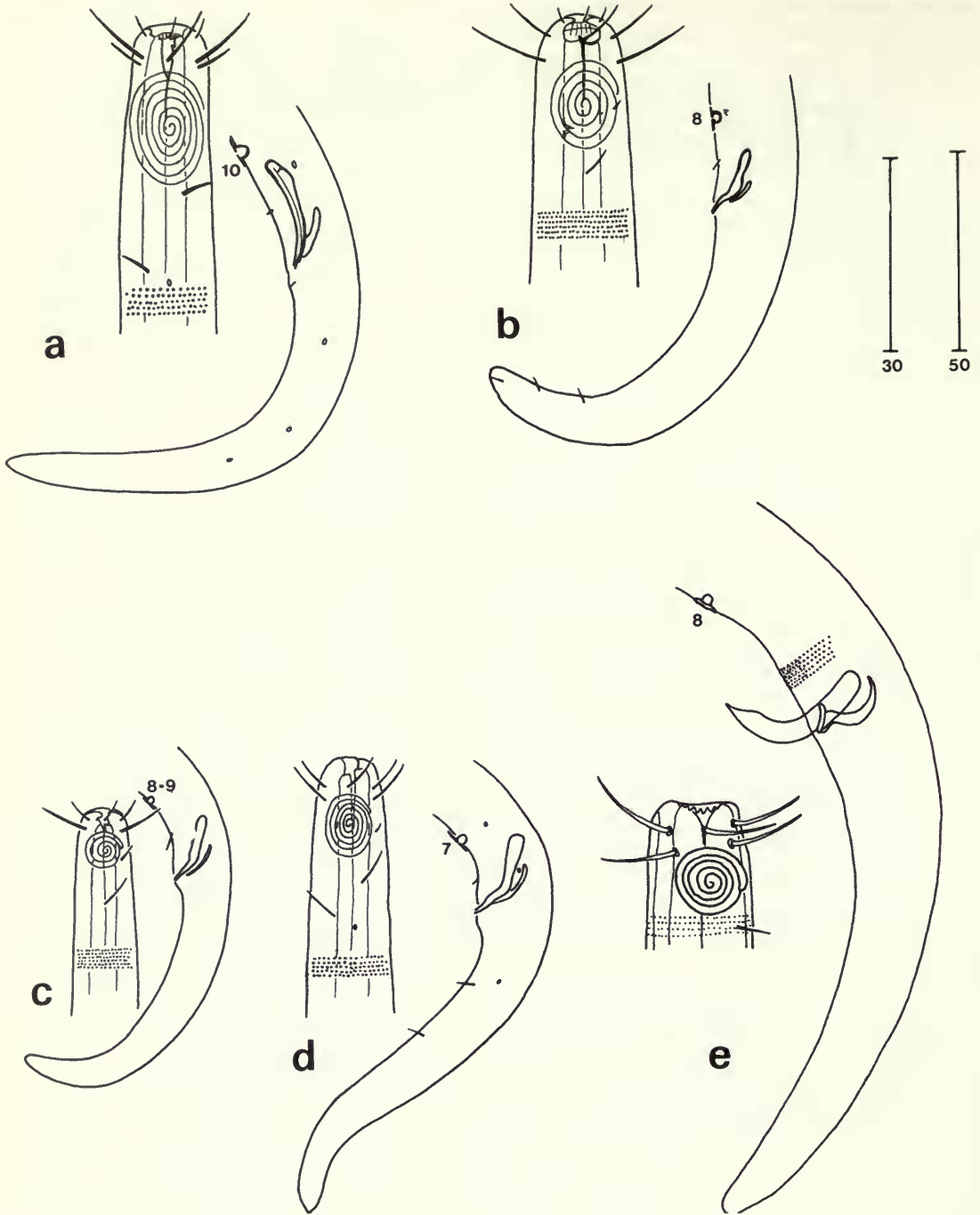


Fig. 5 (a) *Nannolaimus fusus*; (b) *Nannolaimus phaleratus*; (c) *Filitonchus filiformis*; (d) *Filitonchus ewensis*; (e) *Filitonchus volutus* (after Gerlach, 1956). Bar scales as in Fig. 2.

the diagnostic characters, other features shown by the species are: no lateral differentiation; slender body ('a' > 50); R₂ and R₃ sensilla long (> 50% c.d.); amphid large (about 80% c.d. in males); 8–10 supplements. The species can be distinguished using the information in Table 4 and Fig. 5.

The two species of *Nannolaimus* constitute one of the least satisfactory grouping within the Ethmolaimidae. It could be argued that the condition 'R₂ sensilla longer than R₃ sensilla', if discontinuously distinct from 'R₃ sensilla longer than R₂ sensilla', is sufficient grounds for assigning *N. fusus* to different genus from *N. phaleratus*. However, if the length of the two circles of sensilla can vary independently then the condition found in *N. fusus* may be towards one end of a range of variation. With but two valid species, only the discovery of further species will provide an answer to this problem.

FILITONCHUS gen. nov.

TYPE SPECIES. *Neotonchus filiformis* Warwick, 1971.

DIAGNOSIS. Neotonchinae. R₁ sensilla papilliform. R₂ sensilla elongate. Buccal cavity not structurally expanded. Clear patch in vas deferens.

REMARKS. The new genus can be distinguished from *Nannolaimus* only through the absence of setiform R₁ sensilla. There are three valid species: *F. filiformis* (Warwick, 1971) comb. nov., syn. *Neotonchus filiformis* Warwick, 1971; *F. ewensis* sp. nov.; *F. volutus* (Gerlach, 1956) comb. nov., syn. *Nannolaimus volutus* Gerlach, 1956.

In addition to the characters used in the diagnosis, other features of the genus as presently constituted are: no lateral differentiation; slender body ('a' > 80); R₃ sensilla long (> 80% c.d.); amphid large (> 70% c.d. in male); 7–9 supplements. The species may be distinguished using the information given in Table 4 and Fig. 5.

Key to the genera of Neotonchinae

The six genera contained in the subfamily may be distinguished by means of the lattice key (Table 5) based on the valid species contained in each genus.

Table 5 Lattice key to genera of the Neotonchinae

Genus	Character							
	A	B	C	D	E	F	G	H
<i>Gomphionema</i>	1	1	2	2	2	1	2	2
<i>Gomphionchus</i>	2	2	1	2	2	1	2	2
<i>Neotonchus</i>	2	2	2	2	2	2	1	1
<i>Neotonchoides</i>	2	2	2	2	2	2	2	2
<i>Nannolaimus</i>	2	2	2	1	1	2	2	2
<i>Filitonchus</i>	2	2	2	2	1	2	2	2

- A: 1. Oesophagus bulb $\geq 30\%$ total oesophagus length; 2. Oesophagus bulb $< 25\%$ total oesophagus length.
 B: 1. Massive dorsal tooth, buccal cavity length $\geq 1.3 \times$ h.d. at mid-amphid level; 2. Dorsal tooth not massive, buccal cavity length $\leq 1.0 \times$ h.d. at mid-amphid level.
 C: 1. Dorsal tooth extends anteriorly into vestibule; 2. Dorsal tooth does not enter vestibule.
 D: 1. R₁ sensilla setiform; 2. R₁ sensilla papilliform or not visible.
 E: 1. R₂ sensilla $\geq 6 \mu\text{m}$; 2. R₂ sensilla $\leq 5 \mu\text{m}$.
 F: 1. Spicule with lateral piece; 2. Spicule without lateral piece.
 G: 1. Tail end with lateral file small dots; 2. Tail end without lateral file small dots.
 H: 1. Sublateral pore-setae present; 2. Sublateral pore-setae absent.

Summary of proposed taxonomic changes and additions

Valid name	Synonymy
Ethmolaimidae Filipjev & Stekhoven, 1941	Neotonchidae Wieser & Hopper, 1966
<i>Ethmolaimus pratensis</i> De Man, 1880	<i>Ethmolaimus parapratensis</i> Alekseev, Naumova & Dymina, 1979
<i>Trichethmolaimus</i> gen. nov.	<i>Spiliphera hirsuta</i> Gerlach, 1956
<i>Trichethmolaimus hirsutus</i> (Gerlach, 1956)	<i>Gomphonema compacta</i> sensu Riemann & Rachor, 1972 nec Gerlach, 1957
<i>Gomphonema euripus</i> sp. nov.	<i>Heterocyatholaimus</i> Allgen, 1935
<i>Neotonchus</i> Cobb, 1933	<i>Neotonchus chamberlaini</i> sensu Boucher, 1976 nec Wieser & Hopper, 1966
<i>Neotonchus boucheri</i> sp. nov.	
<i>Gomphonchus</i> gen. nov.	<i>Neotonchus lutosus</i> Wieser & Hopper, 1966
<i>Gomphonchus lutosus</i> (Wieser & Hopper, 1966)	
<i>Neotonchoides</i> gen. nov.	<i>Comesa</i> Gerlach, 1956
<i>Neotonchoides melotridus</i> (Wieser & Hopper, 1966)	<i>Neotonchus melotridus</i> Wieser & Hopper, 1966
<i>Neotonchoides corcundus</i> (Gerlach, 1956)	<i>Neotonchus corcundus</i> (Gerlach, 1956)
<i>Neotonchoides vitius</i> (Warwick, 1971)	<i>Neotonchus vitius</i> Warwick, 1971
<i>Neotonchoides interruptus</i> (Warwick, 1971)	<i>Neotonchus interruptus</i> Warwick, 1971
<i>Neotonchoides votadinii</i> (Warwick, 1971)	<i>Neotonchus votadinii</i> Warwick, 1971
<i>Neotonchoides pseudocorcundus</i> (Vitiello, 1971)	<i>Neotonchus pseudocorcundus</i> Vitiello, 1971
<i>Neotonchoides cupulatus</i> (Vitiello, 1971)	<i>Neotonchus cupulatus</i> Vitiello, 1971
<i>Neotonchoides vitielloii</i> sp. nov.	<i>Neotonchus aff. corcundus</i> sensu Vitiello, 1970 nec Gerlach, 1956
<i>Neotonchoides cuanensis</i> sp. nov.	
<i>Neotonchoides warwicki</i> sp. nov.	<i>Neotonchus corcundus</i> sensu Warwick & Buchanan, 1970 nec Gerlach, 1956
<i>Nannolaimus phaleratus</i> (Wieser & Hopper, 1966)	<i>Neotonchus phaleratus</i> Wieser & Hopper, 1966
<i>Filitonchus</i> gen. nov.	
<i>Filitonchus filiformis</i> (Warwick, 1971)	<i>Neotonchus filiformis</i> Warwick, 1971
<i>Filitonchus volutus</i> (Gerlach, 1956)	<i>Nannolaimus volutus</i> Gerlach, 1956
<i>Filitonchus ewensis</i> sp. nov.	
<i>Paralongicyatholaimus complicatus</i> (Gerlach, 1957)	<i>Nannolaimus complicatus</i> Gerlach, 1957

Doubtful taxa

- Ethmolaimus faeroeensis* Ditlevsen, 1928 sp. inq.
Ethmolaimus caudatus Alekseev, Naumova & Dymina, 1979 sp. inq.
Gomphonema compactum Gerlach, 1957 sp. dub.
Neotonchus macrolaimus (Allgen, 1935) sp. dub.
Neotonchus hapalus Vitiello, 1974 nomen nudum
Neotonchus spiralis Vitiello 1974 nomen nudum
Nannolaimus guttatus Cobb, 1920 sp. inq.
Nannolaimus labiosus Vitiello, 1974 nomen nudum

Species descriptions

Trichethmolaimus hirsutus (Gerlach, 1956) comb. nov.
(Fig. 2a)

Spiliphera hirsuta Gerlach, 1956

MATERIAL STUDIED. Several ♂♂, collected by Mr P. J. D. Lamshead.

LOCALITY. Clyde Sea, Scotland.

REMARKS. The specimens were only studied in sufficient detail to ascertain the following features: 10 typical cup-shaped preloacal supplements present; two opposed testes. The fixation-shape is characteristically a tight coil, so that detailed study will be difficult: thus far, few uncoiled specimens have been encountered.

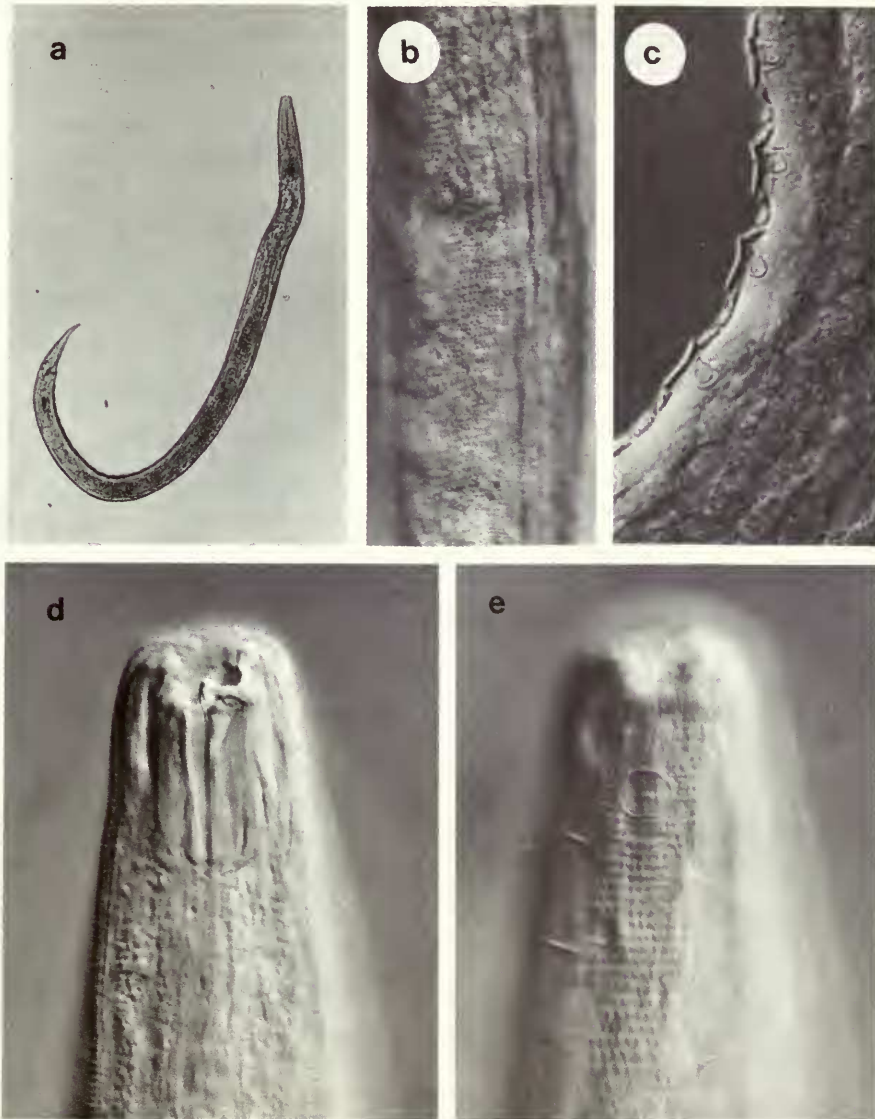


Fig. 6 *Ethmolaimus pratensis*: (a) ♂ whole body; (b) cuticle pattern at mid-body; (c) preloacal supplements; (d) anterior showing buccal cavity; (e) anterior showing amphid.

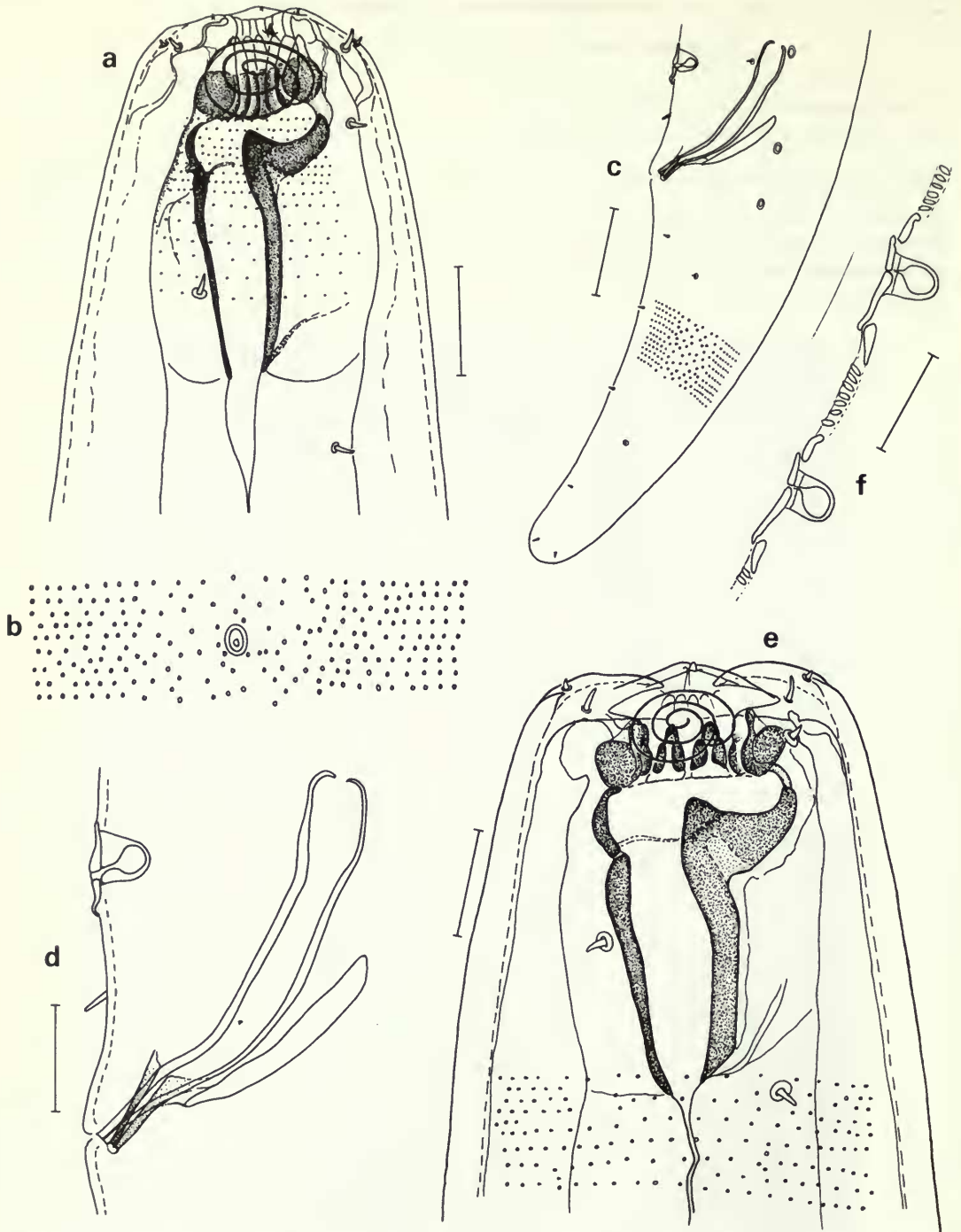


Fig. 7 *Gomphonema typicum*: (a) holotype σ head; (b) cuticle pattern at mid-body; (c) σ tail; (d) copulatory apparatus; (e) q head. *Ethmolaimus pratensis*: (f) supplements. Bar scales: c = 20 μm ; others = 10 μm .

Ethmolaimus pratensis De Man, 1880

(Figs 2b, 6, 7f)

MATERIAL STUDIED. 1 ♂ (slide Tv 134 p), 3 ♀ (slides Tv 134c, e, g) in the collection of Dr P. Jensen.

LOCALITY. Pojoviken, southern Finnish archipelago.

DESCRIPTION. Cuticle with transverse rows of punctations which in the lateral field are larger and arranged in fewer rows, although in places tending to be irregular. This lateral differentiation of fewer rows of larger dots is most noticeable in the region between the amphid and the nerve ring. There is a single lateral file of small cuticle pores; difficult to distinguish. In the male studied, there were 15 supplements which extended 350 μm anterior to the cloaca, 30% of total body length. The anterior testis is to the left, posterior to the right of the gut.

REMARKS. Apart from this additional data, the specimens agree with the redescription by Jensen (1979a). Cobb (1914) noted the more conspicuous lateral punctations near the head of the female specimen he called *E. americanus* (= *E. pratensis*) but could not detect any lateral differentiation.

Gomphonema typicum Wieser & Hopper, 1966

(Figs 2c, 7a-e, 8, 9)

MATERIAL STUDIED. Holotype ♂, slide 121 and allotype ♀, slide 121a, Canadian National Collection of Nematodes.

LOCALITY. Sandflat, Key Biscayne, Florida, U.S.A.

DESCRIPTION.

Holotype ♂: $\frac{- \quad 200 \quad \text{M} \quad 1238}{21 \quad 53 \quad 62 \quad 41}$ 1335 μm ; a = 22; b = 7; c = 14; S = 41 μm

Allotype ♀: $\frac{- \quad 220 \quad 710 \quad 1242}{29 \quad 72 \quad 77 \quad 49}$ 1350 μm ; a = 18; b = 6; c = 13; V = 53%

Cuticle bears transverse rows of punctations and there is a lateral differentiation of fewer rows which begins about the level of the buccal cavity and continues to the tail tip (Figs 7b, 9b). The lateral punctations are irregular throughout most of the body, but in the oesophageal region they are in relatively regular transverse rows. Conspicuous lateral cuticle pores are present: the male had a total of 12 on the right side, 4 in oesophageal region, and 13 on left side, 5 in oesophageal region; the female had a total of 34 on right side, 9 in oesophageal region, and 31 on left side, 8 in oesophageal region. Sparse sublateral spine-like somatic setae present. R_1 sensilla minute papillae. R_2 sensilla papilliform, about 1 μm . R_3 sensilla short setae, about 2 μm , situated only slightly posterior to R_2 sensilla (Figs 7a, e). Short dorso-sublateral subcephalic setae present. Amphid 3+ turns in both sexes, situated anteriorly on head and therefore appearing oval in lateral view: 10.5 μm (45% c.d.) wide in male; 10 μm (30% c.d.) wide in female. Buccal cavity larger and more heavily cuticularised in female than male (Figs 7a, e). 12 well-developed rugae at anterior of buccal cavity which appear to be organised in six pairs at certain depths of focus (Fig. 7e). Massive dorsal tooth. Large oesophageal bulb, constituting 33% and 44% of oesophagus length in male and female respectively. Tail conical with two small ventro-sublateral spines in both sexes and short subventral setae in male (Fig. 7c). Spicules slightly cephalate proximally and in addition to the dorsal gubernaculum there is an extra structure lying lateral to the distal end of each spicule (Fig. 7d). Precloacal spine present and 22 precloacal supplements extending 395 μm anterior to cloaca (Figs 9c, d). No clear patch in vas deferens detected. Two opposed testes; anterior left, posterior right of gut. Two opposed, reflexed ovaries; anterior lies left of gut and is reflexed to the right, posterior lies right of gut and is reflexed to the left.

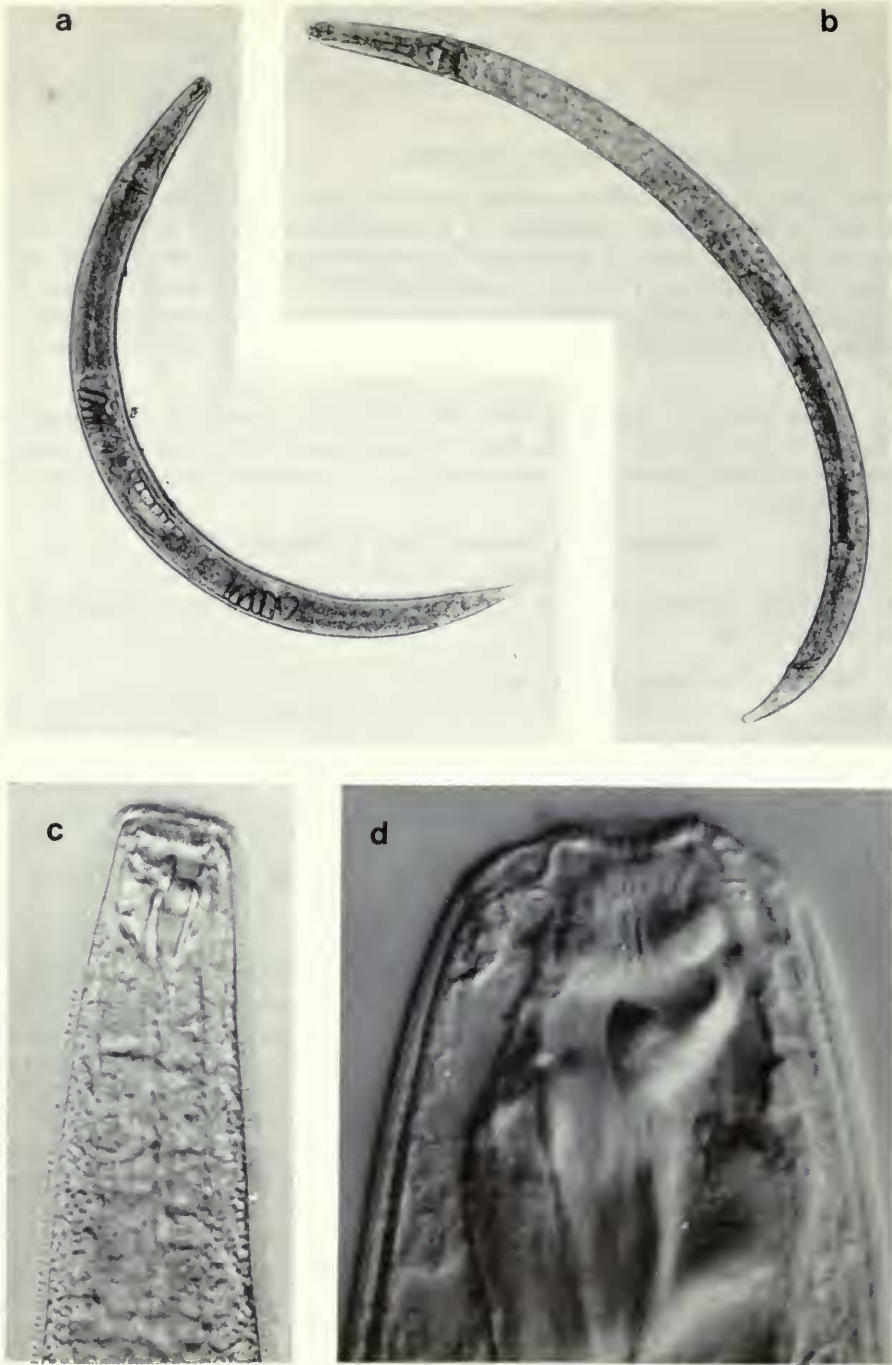


Fig. 8 *Gomphonema typicum*: (a) allotype ♀ whole body; (b) holotype ♂ whole body; (c) allotype anterior region; (d) holotype head.

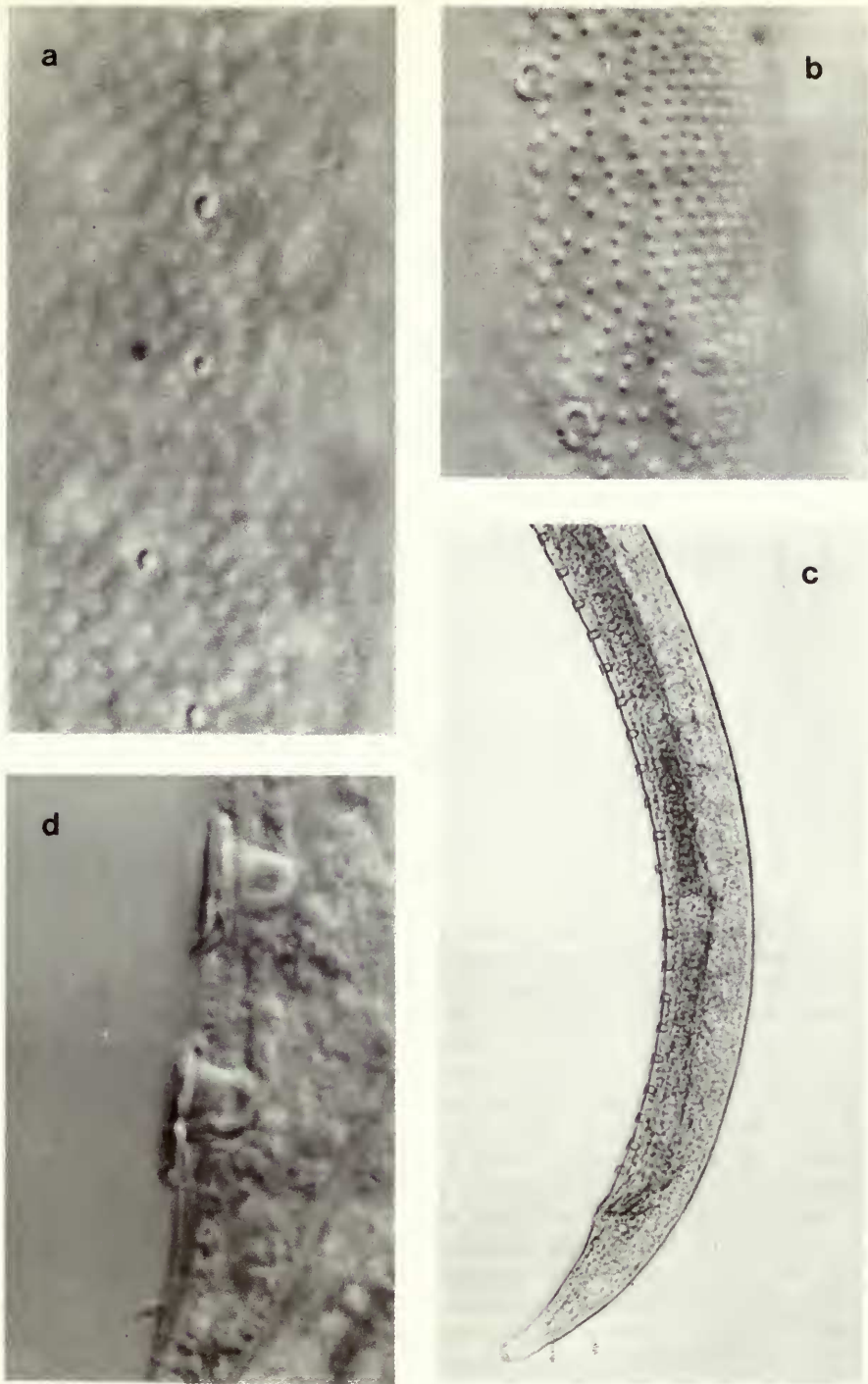


Fig. 9 *Gomphonema typicum*: (a) ♀ lateral cuticle showing pores; (b) ♀ lateral cuticle showing differentiation; (c) ♂ posterior region; (d) preloacal spine and two preloacal supplements.

REMARKS. There are some points of difference between the description given above and that of Wieser & Hopper (1966), although the latter is based on a large number of specimens. The R_2 and R_3 sensilla are not in one circle; the R_3 are slightly posterior to the R_2 . The cuticular punctation is not of 'uniform distribution over entire body', if this statement is taken to imply an absence of lateral differentiation. Wieser & Hopper (1966) quote the range of maximum width as 78–90 μm : the holotype has a maximum diameter of 62 μm . The female studied here had almost three times as many cuticle pores as the male but whether this reflects a true sexual dimorphism is obviously unclear. Also, the allotype has a more substantial buccal cavity. Finally, there are two testes, not one.

Gomphonema fellator Wieser & Hopper, 1966
(Figs 2d, 10–12)

MATERIAL STUDIED. Holotype σ_1 (slide 122), allotype φ_1 (slide 122a), paratype σ_2 (slide 122b) and paratypes σ_3, φ_{2-5} (slide 122e), Canadian National Collection of Nematodes.

LOCALITY. σ_{1-2}, φ_1 from muddy sand, Charleston, South Carolina, U.S.A.; σ_3, φ_{2-5} from Sapelo Island, Georgia, U.S.A.

DESCRIPTION.

Holotype σ_1 : $\frac{-}{16} \frac{203}{41} \frac{M}{41} \frac{974}{30}$ 1040 μm ; a = 25; b = 5; c = 16; S = 36 μm .

Allotype φ_1 : $\frac{-}{17} \frac{215}{49} \frac{486}{56} \frac{865}{35}$ 930 μm ; a = 17; b = 4; c = 14; V = 52%

Paratype σ_2 : L = 1035 μm ; a = 26; b = 5; c = 15; S = 38 μm

Paratype σ_3 : L = 645 μm ; a = 18; b = 5; c = 13; S = 36 μm

Paratype φ_2 : L = 593 μm ; a = 15; b = 4; c = 11; V = 54%

Paratype φ_3 : L = 672 μm ; a = 18; b = 5; c = 14; V = 57%

Paratype φ_4 : L = 734 μm ; a = 18; b = 5; c = 15; V = 55%

Paratype φ_5 : L = 924 μm ; a = 21; b = 6; c = 17; V = 66%

Cuticle bears transverse rows of punctations and the lateral dots are larger. The lateral dots are not much larger in most of the oesophageal region but towards the end of the oesophagus, the lateral dots become larger and slightly irregular (Fig. 10b). By about the middle of the body, the lateral dots are conspicuously larger and although irregular, give the appearance of being in fewer transverse rows (Fig. 10c). This lateral differentiation of fewer rows ends just anterior to the tail, although the lateral dots are still larger on the tail. There are numerous small lateral cuticle pores present from the mid-oesophageal level to mid-caudal level (Figs 10b, d and 12b). Short sublateral spine-like somatic setae present. R_1 sensilla minute. R_2 sensilla papillate. R_3 sensilla short, about 1 μm . Short dorso-sublateral subcephalic seta present. Amphid 3+ turns in both sexes, about 8–9 μm wide and transversely oval in Charleston specimens (Fig. 10a), but more rounded in Sapelo Island specimens (Fig. 10f). Buccal cavity similar to *G. typicum*, although the large dorsal tooth is more pointed and anteriorly directed (Fig. 11d). Large oesophageal bulb (Fig. 11c), 31–36% of oesophageal length with no apparent sexual dimorphism. Tail conical with 3 ventro-sublateral and 2 dorso-sublateral spines. In the males, there are also 3, sometimes 4, subventral spines (Fig. 10d); absent in females. Spicules have extra lateral pieces at the distal ends (Figs 10e, g). Precloacal spine present, emanating from a conspicuous base structure (Fig. 10e). 15 precloacal supplements, extending in σ_1 298 μm , in σ_2 320 μm and in σ_3 192 μm anterior to cloaca, but occupying about 30% of the total body length in each case. Two opposed testes; anterior left, posterior right of gut. No clear patch in vas deferens. Two opposed, reflexed ovaries; anterior lies left of gut and reflexed to the left, posterior lies right of gut and reflexed to the right.

REMARKS. There are some points of difference between the description given above and that of Wieser & Hopper (1966): the cephalic setae are not in one circle; the cuticle punctuation is not uniform all along the body; cuticle pores are present. Otherwise the information given in Wieser & Hopper (1966) is corroborated here. *G. fellator* can be distinguished from *G. typica* in having more numerous cuticle pores, lateral differentiation not present in oesophageal region, fewer preloacal supplements and a preloacal spine with a conspicuous base.

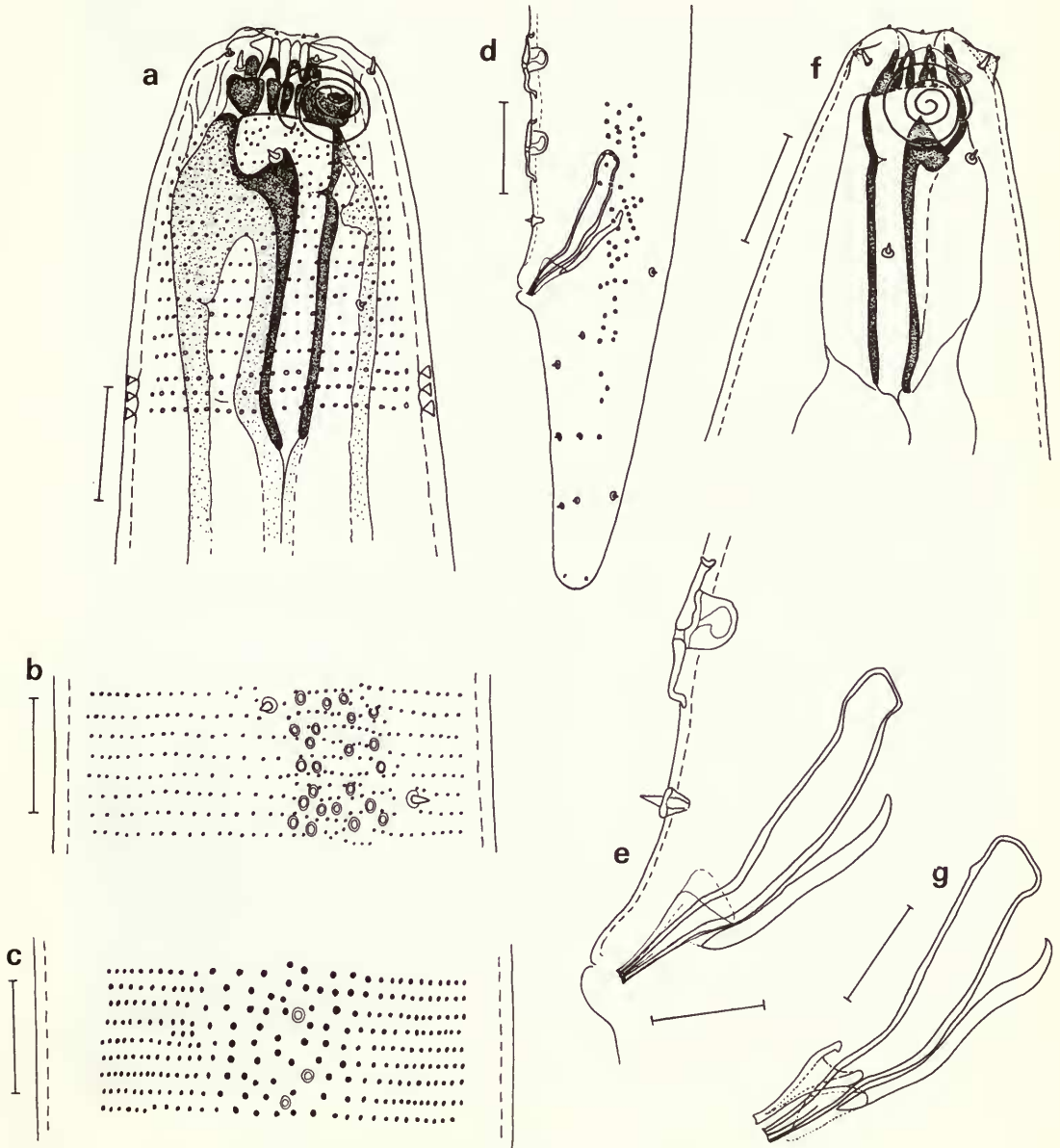


Fig. 10 *Gomphonema fellator*: (a) holotype σ head; (b) cuticle pattern level with anterior of oesophageal bulb, dorso-sublateral view showing cuticle pores and sublateral spines; (c) cuticle pattern mid-body, lateral view showing differentiation; (d) holotype σ tail; (e) holotype copulatory apparatus; (f) paratype σ , head; (g) paratype σ , copulatory apparatus. Bar scales: d = 20 μ m; others = 10 μ m.

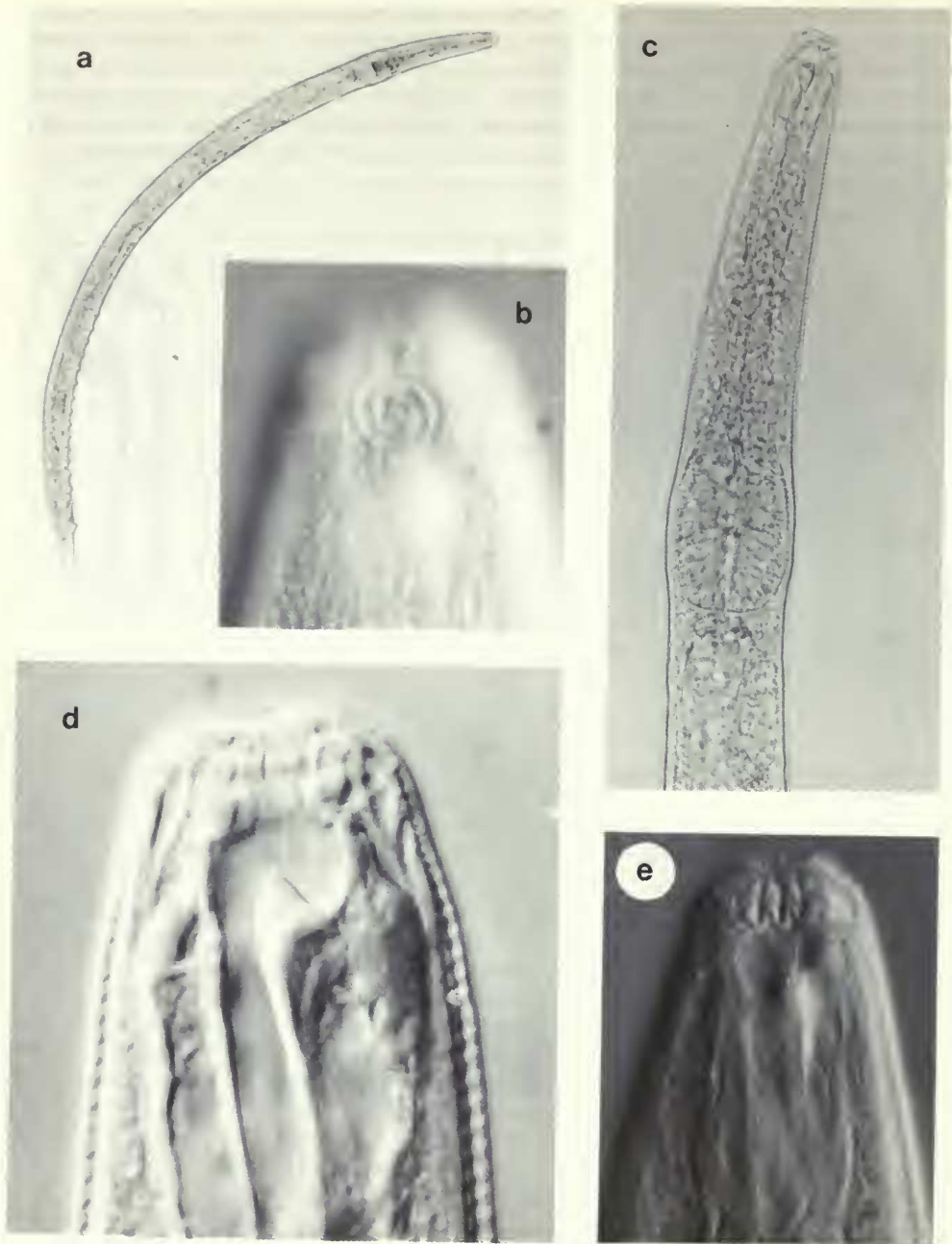


Fig. 11 *Gomphiozema fellator*: (a) holotype σ whole body; (b) head showing amphid; (c) anterior region; (d) head showing buccal cavity; (e) head showing rugae.

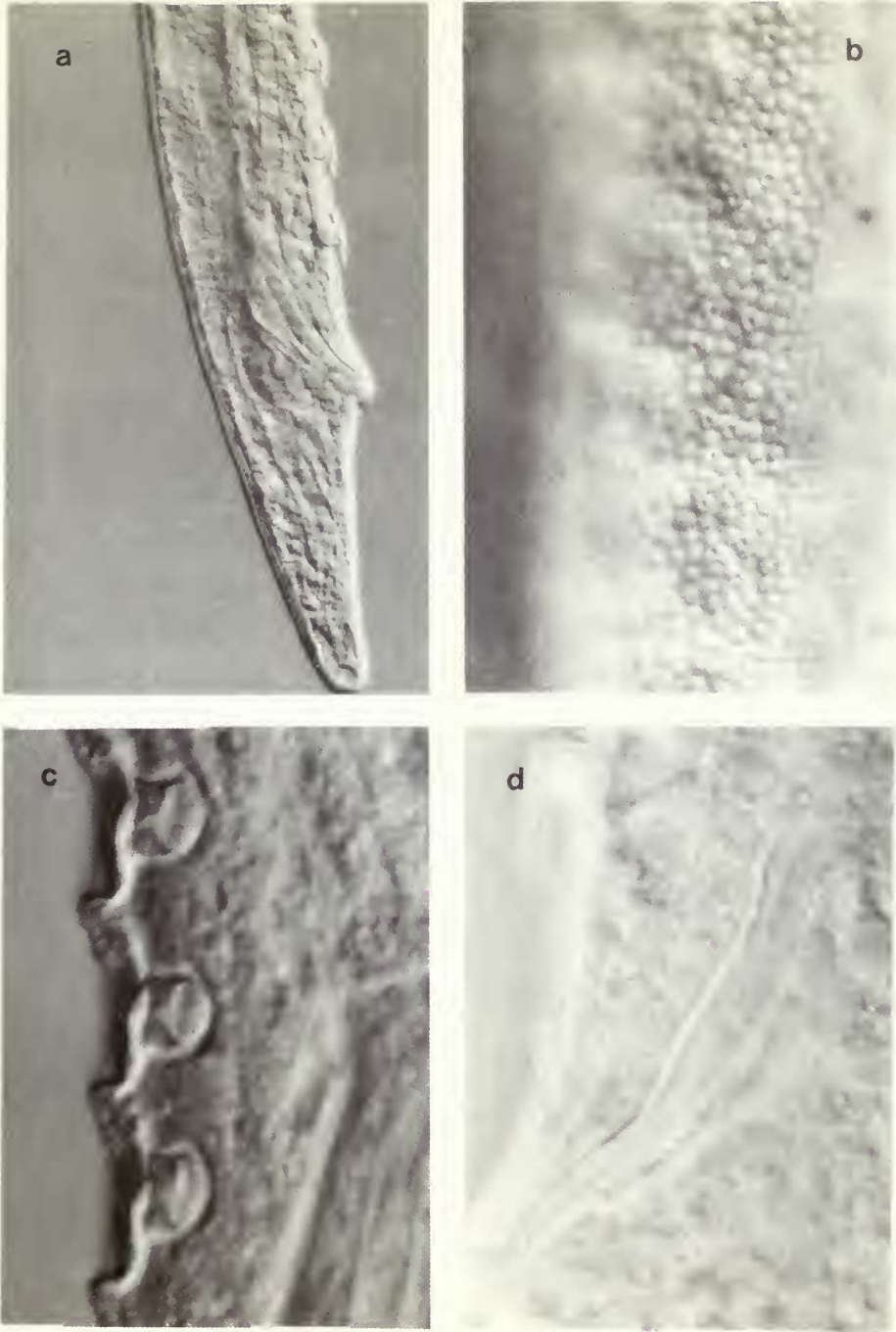


Fig. 12 *Gomphonema fellator*: (a) holotype ♂ tail; (b) lateral cuticle showing pores; (c) precloacal supplements of another ♂; (d) spicule.

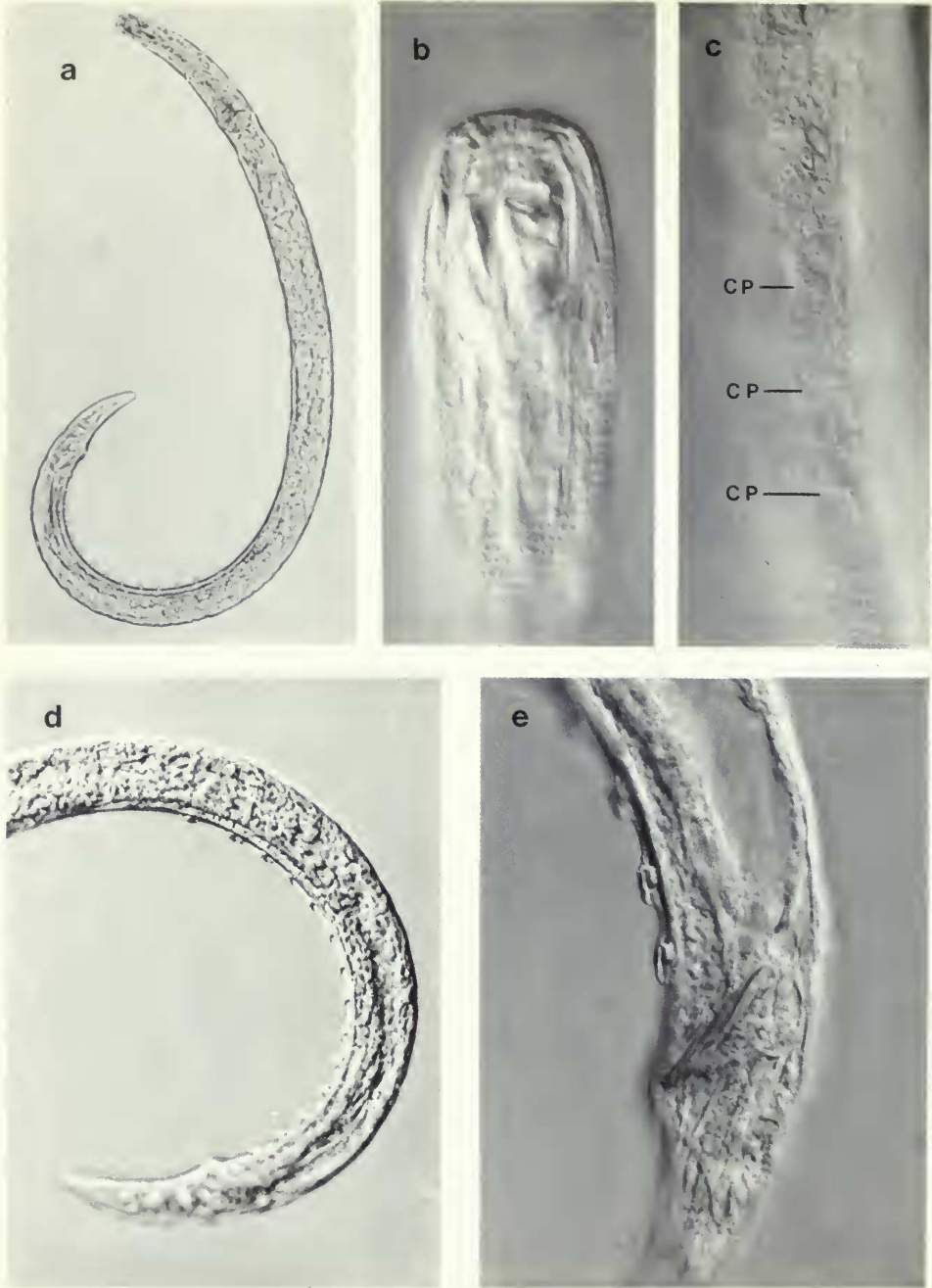


Fig. 13 *Gomphonema* sp.: (a) ♂ whole body; (b) head showing buccal cavity; (c) lateral cuticle punctations, CP = cuticle pore; (d) ♂ posterior region; (e) cloacal region.

Gomphonema sp.
(Figs 2e, 13)

A new species of *Gomphonema* was found by Dr R. M. Warwick in Australia and he will be providing a description. However, he kindly allowed some specimens to be observed and photographed in order that the species could be included in this work. The following information is given simply to indicate the state of those characters of phylogenetic importance.

DESCRIPTION. Lateral differentiation present, consisting of larger dots and fewer transverse rows (Fig. 13c) and beginning posterior to oesophageal region. The lateral rows of dots appear to anastomose in places. Minute cuticle pores present as a single lateral row 13–15 μm apart (Fig. 13c): difficult to detect. Sublateral somatic spine-like setae present. Lateral spicule pieces present. Precloacal spine and 14 precloacal supplements present. Two opposed testes; anterior right, posterior left of gut. No clear patch in vas deferens. The male tail has two dorso-sublateral, two larger ventro-sublateral spines and three sub-ventral spines.

REMARKS. The specimens can be distinguished from the other two valid species by the cuticle pores, fewer than *G. fellator* and smaller than *G. typica*, in addition to several other minor differences.

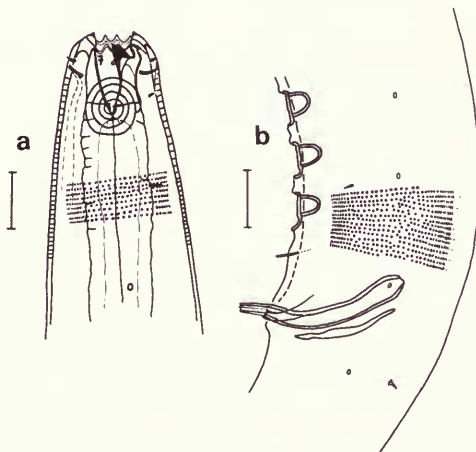


Fig. 14 *Gomphonchus lutosus*: (a) holotype σ head; (b) holotype cloacal region. Bar scales: 10 μm .

Gomphonchus lutosus (Wieser & Hopper, 1966) comb. nov.
(Figs 3e, 14, 15)

Neotonchus lutosus Wieser & Hopper, 1966.

MATERIAL STUDIED. Holotype σ , slide 91, Canadian National Collection of Nematodes.

LOCALITY. Mud, Virginia Key, Florida, U.S.A.

DESCRIPTION. Cuticle with transverse rows of punctations. True lateral differentiation of fewer rows of dots is absent although in the lateral field the rows tend to anastomose, so that in places there can seem like fewer rows. A lateral file of small cuticle pores present, about 15 μm apart, from the anterior oesophageal region to the tail (Figs 3e, 14b, 15b, c). Sublateral

somatic setae present. Dorso-sublateral subcephalic seta present situated just anterior to the middle of the amphid (Fig. 15e). R_3 sensilla situated level with the anterior of the amphid. Amphid of 4+ turns. Excretory pore 7 μm from anterior (Fig. 14a). Spicules have an extra piece lateral to distal end (Fig. 15h). The preloacal spine is situated closer to the first supplement than the cloaca (Fig. 14b). 20 preloacal supplements. Two opposed testes; anterior left, posterior right of gut. A possible clear patch in the vas deferens was observed lying between the levels of supplements 5–7 (Fig. 15d).

REMARKS. The disposition of the cephalic sensilla reported here is slightly different from that depicted by Wieser & Hopper (1966); the latter placed the two R_3 sensilla at the level where the dorso-sublateral subcephalic seta were observed here. Wieser & Hopper (1966) also depicted the excretory pore 40 μm from the anterior whilst it was found only 7 μm from the anterior in this study, level with the R_2 sensilla. Otherwise, the observations reported here conform well with the original description.

Neotonchus punctatus Cobb, 1933
(Figs 3a, 16, 17)

MATERIAL STUDIED. 1 σ , slide T-69 t (Lectotype), U.S. Department of Agriculture Nematode Collection.

LOCALITY. Cuttyhunk Hole, Woods Hole, Massachusetts, U.S.A.

DESCRIPTION.

$$\sigma: \frac{-}{13} \frac{102}{30} \frac{M}{[26]} \frac{646}{24} 722 \mu\text{m}; a = 28; b = 7; c = 10$$

Body slightly larger than reported by Wieser & Hopper (1966). The specimen is clearly somewhat squashed: since its present maximum dorso-ventral diameter is about 30 μm and the lateral diameter at that point is 22 μm the original diameter is estimated to have been about 26 μm (if the body was cylindrical), giving a higher 'a' ratio – this figure is used in the formula given above. The transverse rows of punctations show no lateral differentiation in the anterior oesophageal region (Fig. 17b), but about the level of the posterior oesophageal bulb the transverse rows become more widely spaced and irregular. On the posterior part of the tail, there is a lateral longitudinal file of small, closely spaced punctations (Fig. 16a). There are several sublateral cuticle pores, each associated with a more medial and anteriorly situated stout seta – the sublateral pore-seta complexes. The condition of the specimen, covered by oil-droplets, made these structures difficult to observe but the pore-complexes seem to be bilaterally arranged and the distribution observed is shown in Fig. 16a. R_1 sensilla fine, less than 1 μm . R_2 sensilla setiform, 1.5 μm . R_3 sensilla setiform, 3 μm . Dorso-sublateral subcephalic seta 2 μm , level with posterior margin of amphid (Fig. 16b). Amphid of 3+ turns (σ), 9 μm wide (60% c.d.). Spicules 20 μm long with proximal end level with posterior supplement. Short preloacal spine present. 8 typical preloacal supplements extending 110 μm anterior to cloaca. Two testes, both situated to right of gut, opposed and out-stretched: anterior testis larger than posterior testis (Fig. 16a). A clear patch in the vas deferens could not be detected, although a small number of differentiated cells was present where a clear patch might be expected.

REMARKS. This species was first described by Cobb (1933) without any illustrations and subsequently redescribed well by Wieser & Hopper (1966) from Cobb's original material. The foregoing is therefore only a brief redescription based on Cobb's material intended to highlight new information or where observations here are at variance with those of Wieser & Hopper (1966). For example, the cuticle pores had not been detected previously but the lateral file of punctations on the tail had been reported by Cobb (1933) although not by Wieser & Hopper (1966).

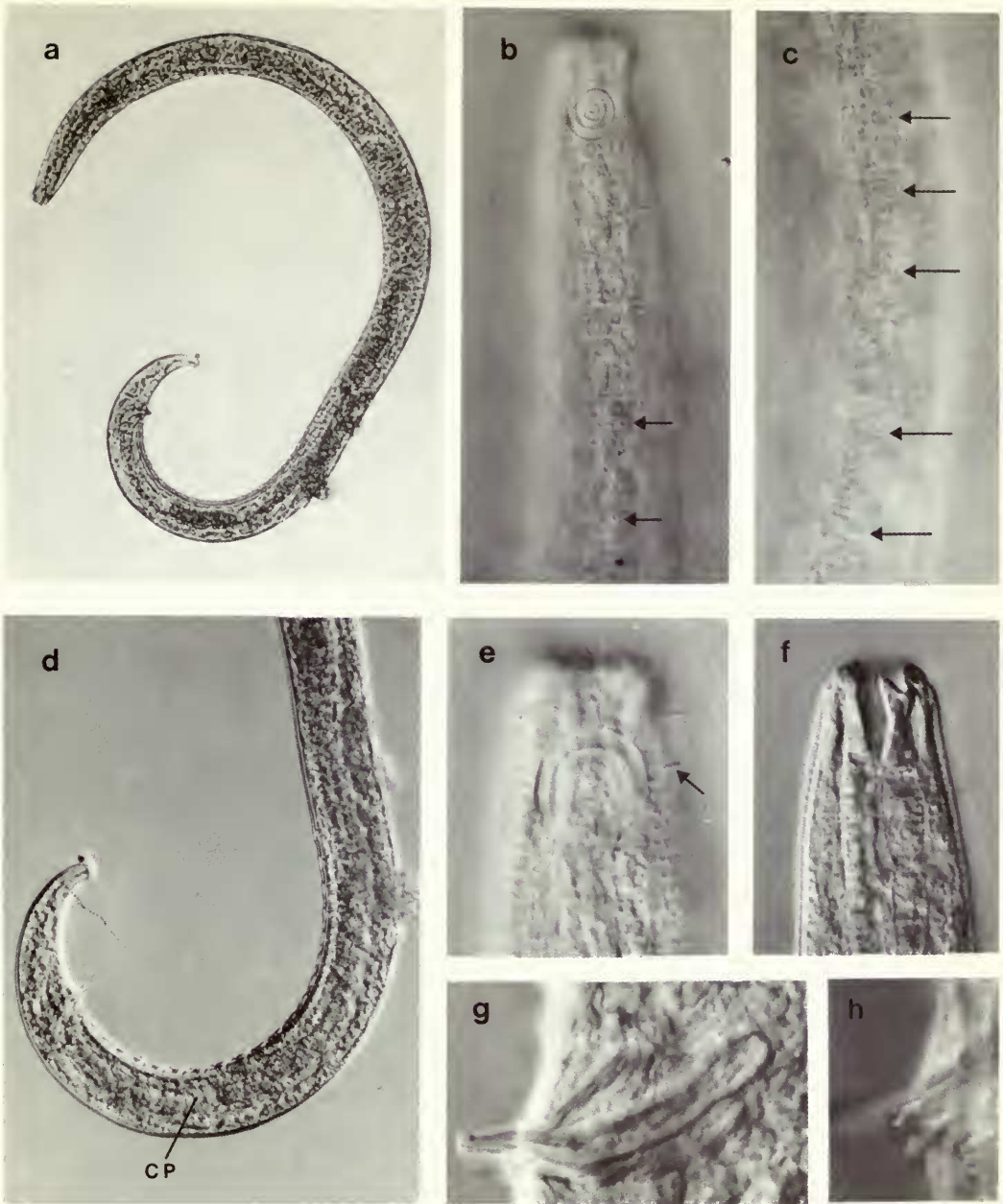


Fig. 15 *Gomphionchus lutosus*: (a) whole body; (b) anterior region, cuticle pores arrowed; (c) lateral mid-body cuticle, cuticle pores arrowed; (d) ♂ posterior region, CP = clear patch; (e) head showing R_3 sensilla and dorso-sublateral subcephalic seta (arrowed); (f) head showing buccal cavity; (g) spicule; (h) lateral spicule piece.

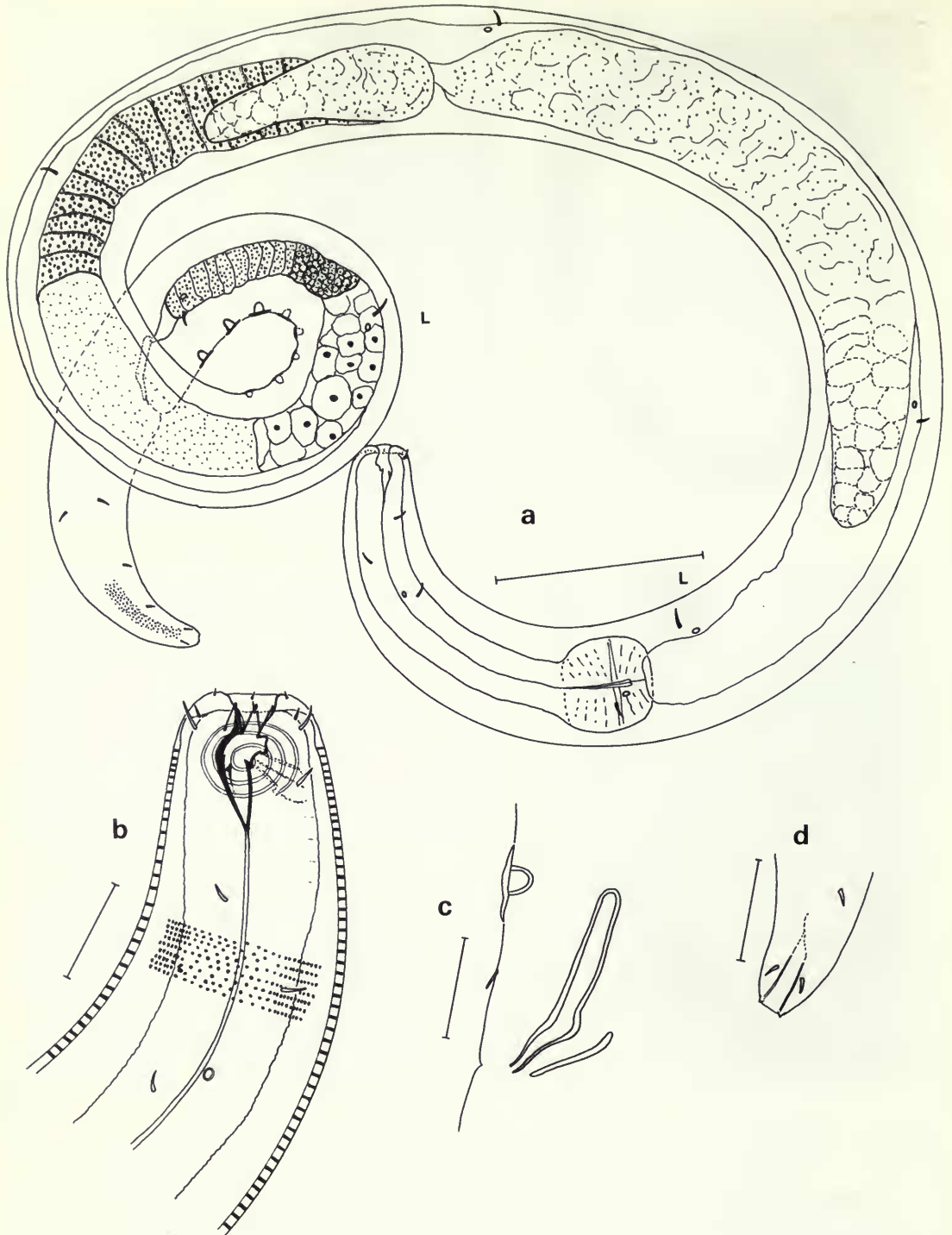


Fig. 16 *Neotonchus punctatus*: (a) whole body (L = position of pore-seta complexes seen on left side only); (b) ♂ head; (c) copulatory apparatus; (d) tail tip. Bar scales: a = 50 μ m; b-d = 10 μ m.

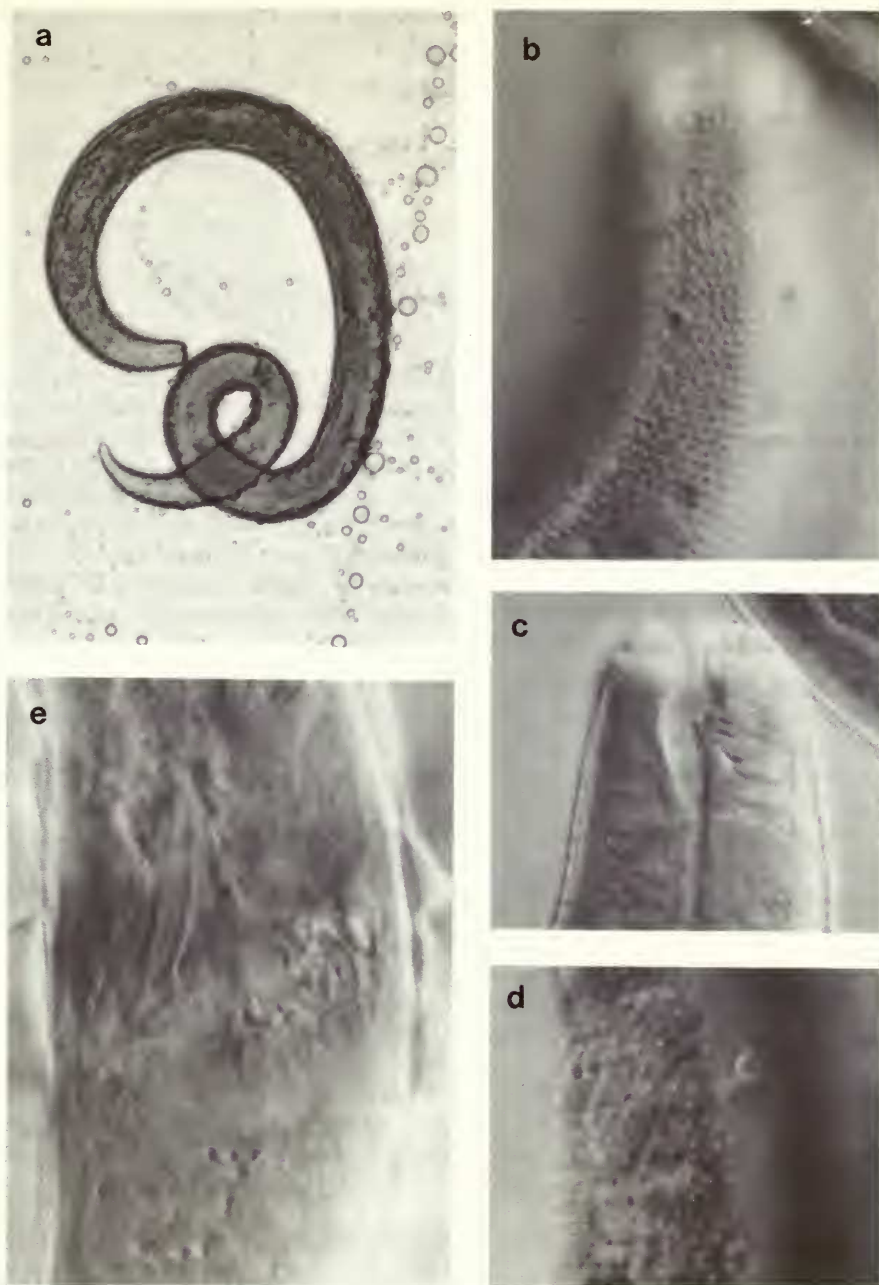


Fig. 17 *Neotonchus punctatus*: (a) whole body; (b) amphid and anterior oesophageal cuticle punctation; (c) buccal cavity; (d) lateral cuticle punctation at mid-body; (e) cloacal region showing spicule.

Neotonchus chamberlaini Wieser & Hopper, 1966
(Figs 3b, 18, 19)

MATERIAL STUDIED. Holotype ♂, slide 118 and paratype ♂, slide 118a; Canadian National Collection of Nematodes.

LOCALITY. 4 miles southeast of the mouth of the North Edisto River, South Carolina, U.S.A. at a depth of 12 m.

DESCRIPTION.

Holotype ♂: $\frac{-}{18} \frac{130}{28} \frac{M}{33} \frac{840}{26}$ 960 μm ; a = 29; b = 7; c = 8

Lateral differentiation of fewer transverse rows of punctations begins level with the posterior end of the oesophagus. Posterior third of tail has lateral longitudinal file of punctations (Fig. 19g). There is a single row of lateral cuticle pores in the oesophageal region and posterior to the oesophagus, sublateral pore-seta complexes are present (Figs 18d, 19c-d). R₁ sensilla are short setae. R₂ sensilla 4 μm . R₃ sensilla 5.5 μm . Short dorso-sublateral subcephalic seta present (Fig. 18a). Male amphid 5+ turns, 14 μm (72% c.d.) wide. Buccal cavity with dorsal and two subventral teeth (Figs 18a, 19f). Spicules 27 μm . 8 (holotype) or 9 (paratype) precloacal supplements extending 125 μm anterior to cloaca (holotype). Precloacal spine present. Clear patch in vas deferens situated level with supplements 5-6. Two opposed testes; anterior to right, posterior to left of gut.

REMARKS. Wieser & Hopper (1966) depicted a single cuticular pore just posterior to the amphid (their Fig. 3) but did not draw attention to it in the text. Neither did they mention the lateral differentiation but they did see the dorso-sublateral subcephalic setae. The amphid has almost one more turn than originally depicted and the paratype one more precloacal supplement. Wieser & Hopper (1966) considered the species was closely related to *Nannolaimus phaleratus* (= *Neotonchus phaleratus*), which it is clearly not. In fact, *N. chamberlaini* is most similar to *N. punctatus* (buccal cavity, lateral differentiation, tail punctations) although it can be easily distinguished using the information in Table 2.

Neotonchus boucheri sp. nov.
(Figs 3c, 20-22)

Neotonchus chamberlaini sensu Boucher, 1976 nec Wieser & Hopper, 1966.

MATERIAL STUDIED. Holotype: ♂R1010, BM(NH)1981.6.63; allotype ♀R162, BM(NH)1981.6.64; paratype ♀R549, BM(NH)1981.6.65; paratype ♂R528, in possession of Dr Boucher.

LOCALITY. Pierre Noire (West Channel), France, sublittoral fine sand; collected by Dr Boucher.

DESCRIPTION.

Holotype ♂: $\frac{-}{15} \frac{120}{21} \frac{M}{22} \frac{683}{20}$ 755 μm ; a = 34; b = 6; c = 11

Paratype ♂: $\frac{-}{16} \frac{110}{20} \frac{M}{22} \frac{643}{19}$ 710 μm ; a = 32; b = 7; c = 11

Allotype ♀: $\frac{-}{15} \frac{91}{21} \frac{312}{25} \frac{528}{19}$ 590 μm ; a = 24; b = 7; c = 9

Paratype ♀: $\frac{-}{16} \frac{110}{24} \frac{360}{25} \frac{597}{20}$ 665 μm ; a = 27; b = 6; c = 10

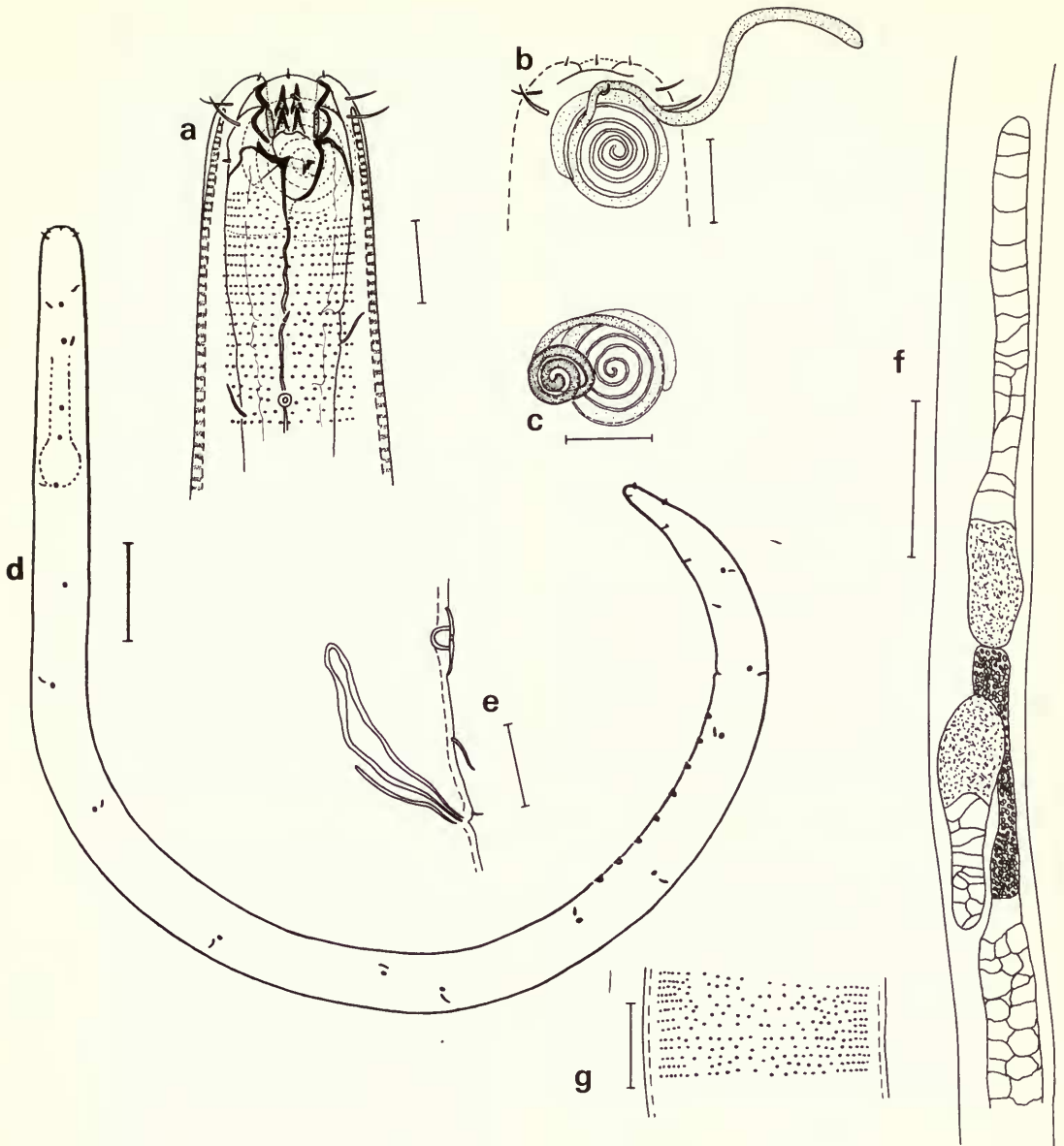


Fig. 18 *Neotonchus chamberlaini*: (a) holotype head; (b) holotype right amphid; (c) holotype left amphid; (d) holotype whole body showing distribution of cuticle pores; (e) holotype copulatory apparatus; (f) paratype σ reproductive system, ventral view, anterior to top; (g) cuticle punctation in cloacal region. Bar scales: a, b, c, e, g = 10 μ m; d, f = 50 μ m.

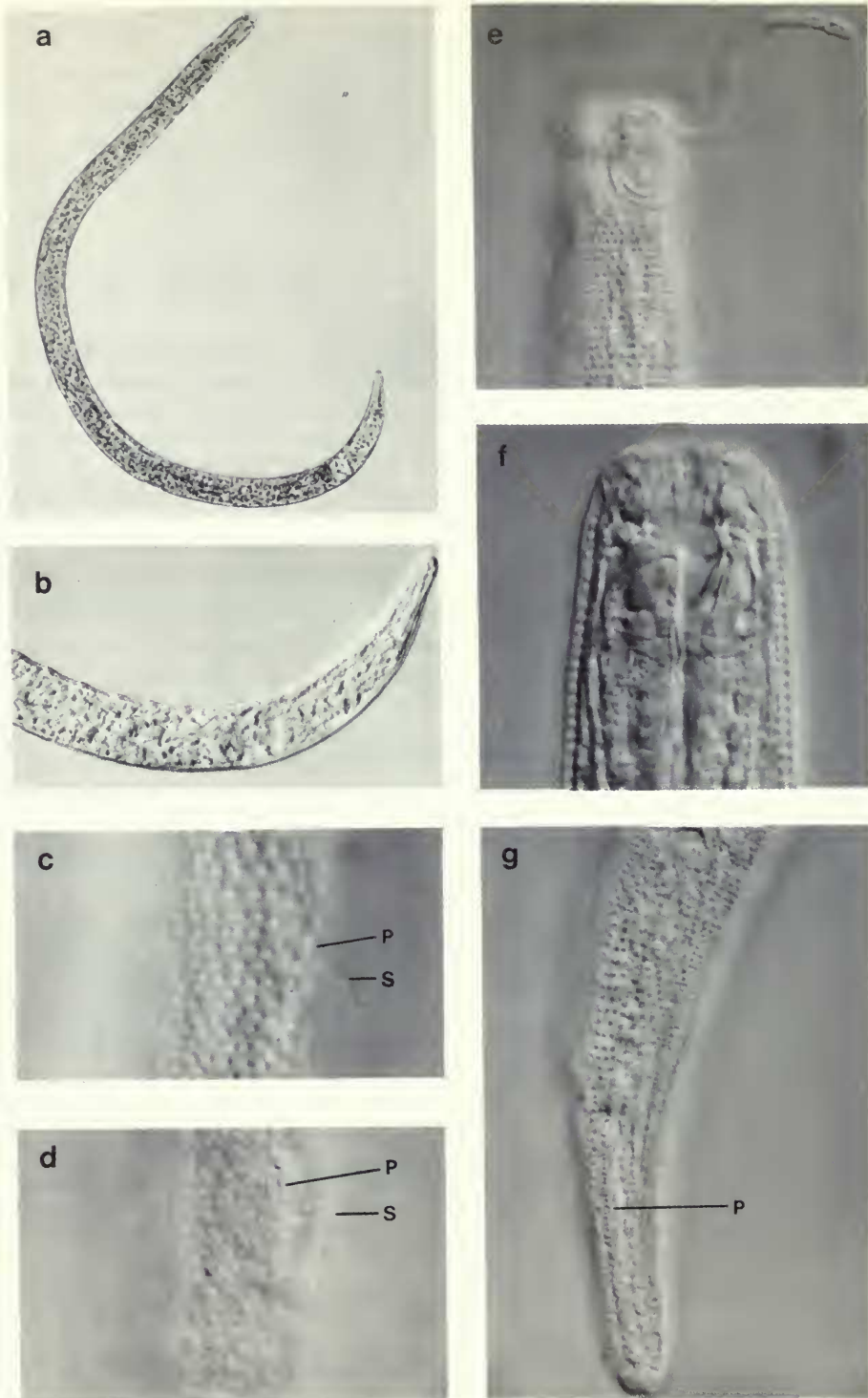


Fig. 19 *Neotonchus chamberlaini*: (a) whole body; (b) tail region; (c) lateral cuticle punctations and pore (P)–seta (S) complex; (d) pore (P)–seta (S) complex; (e) head region showing amphid and anterior cuticle pattern; (f) buccal cavity; (g) tail showing lateral punctations (P).

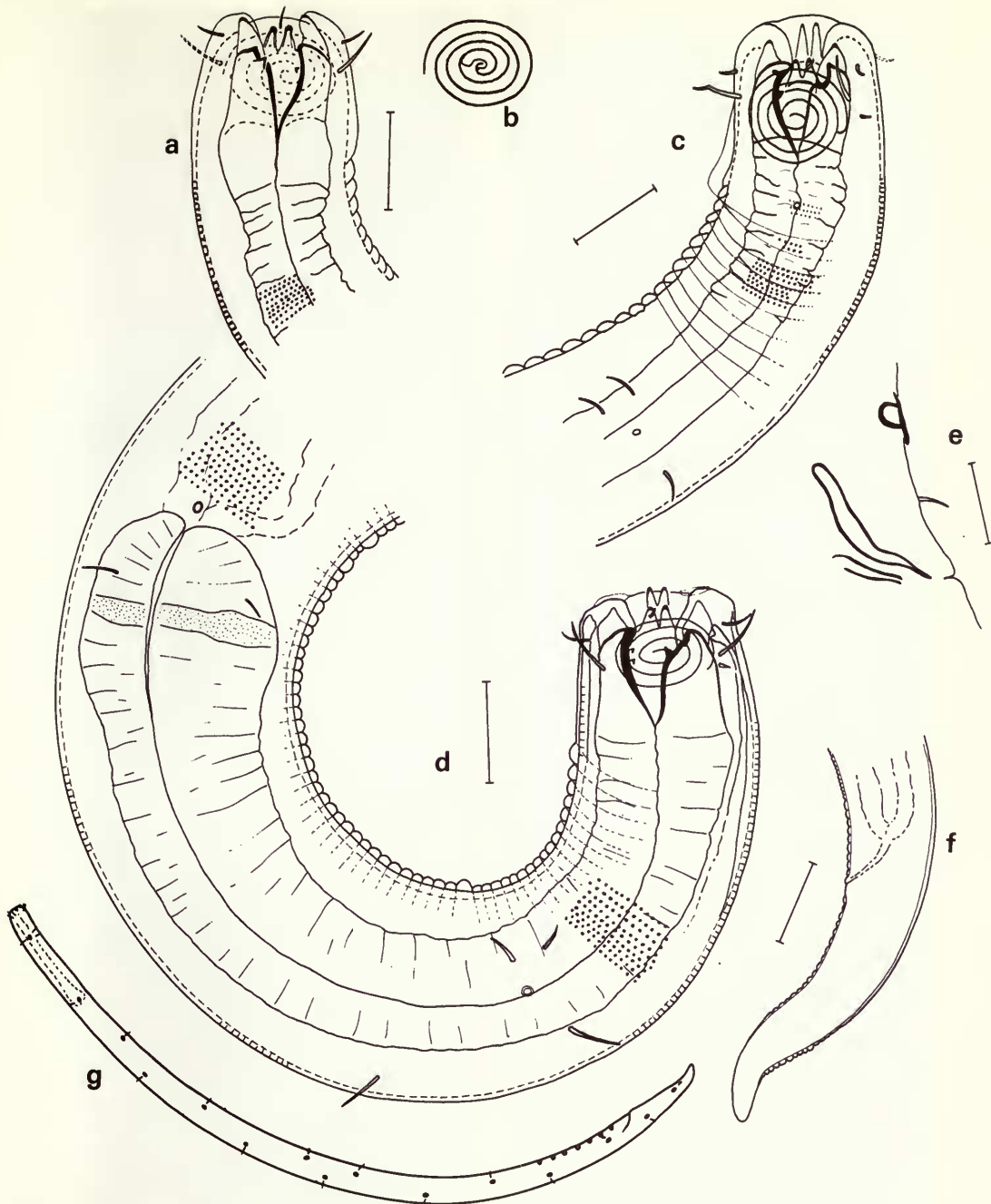


Fig. 20 *Neotonchus boucheri*: (a) head ♂ 528; (b) amphid ♂ 528; (c) head ♂ 1010; (d) anterior ♀ 549; (e) copulatory apparatus ♂ 528; (f) tail ♀ 549; (g) diagrammatic whole body to show distribution of pore-setae (not to scale). Bar scales: a, c, d, e = 10 μ m; f = 20 μ m.

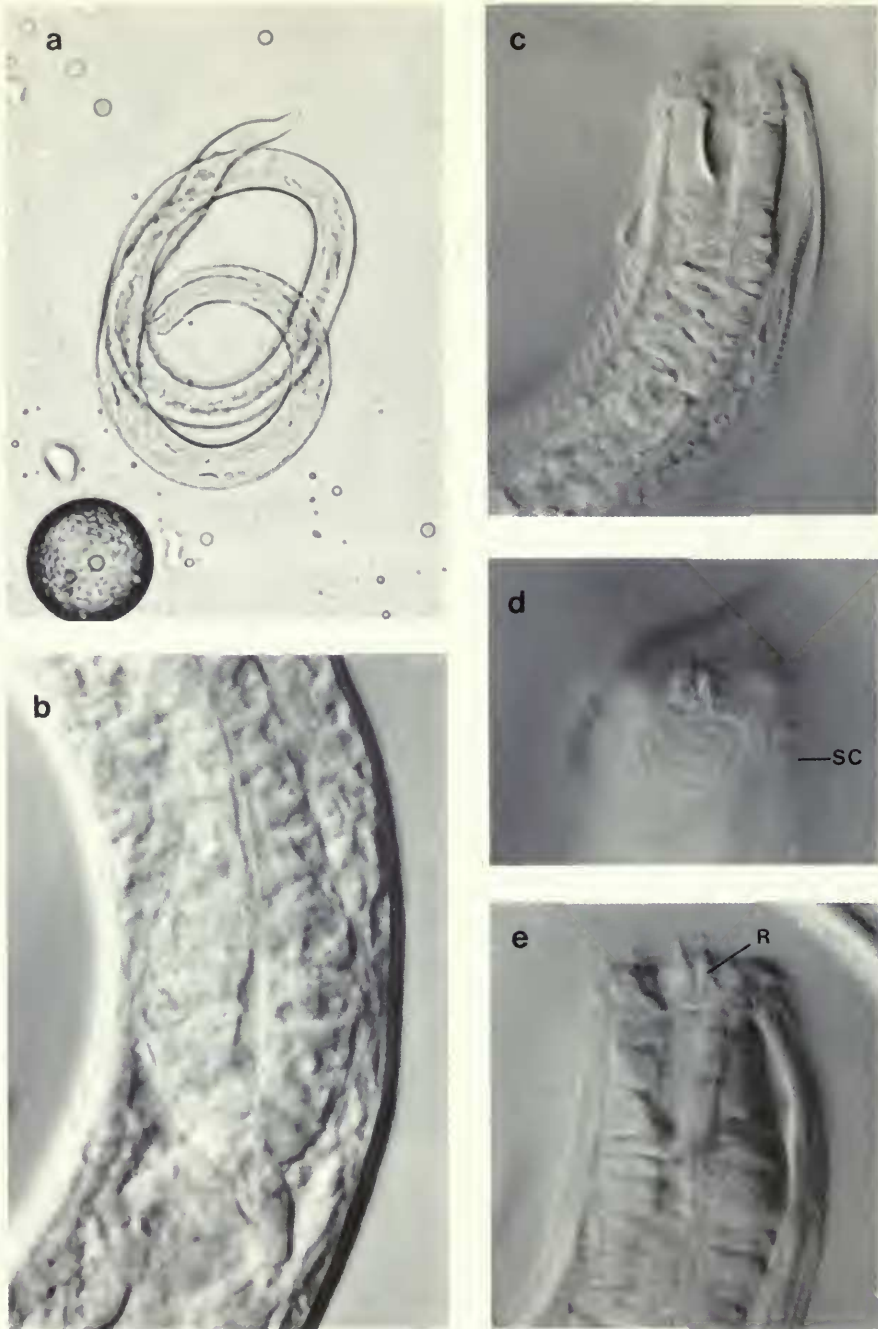


Fig. 21 *Neotonchus boucheri*: (a) whole body; (b) posterior oesophagus bulb; (c) buccal cavity; (d) amphid, cephalic setae and dorso-sublateral subcephalic seta (SC); (e) anterior part of buccal cavity showing buccal rugae (R).

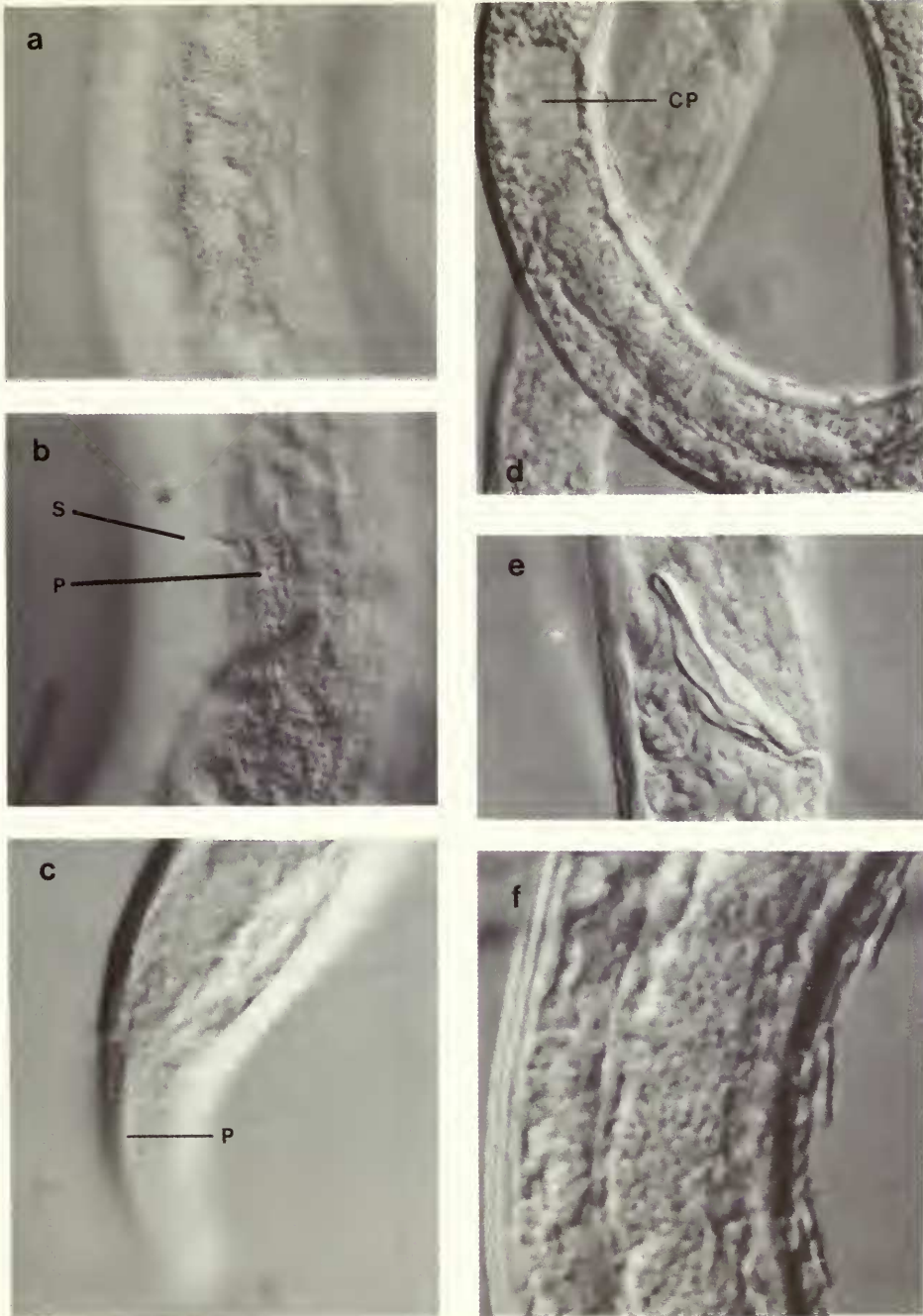


Fig. 22 *Neotonchus boucheri*: (a) lateral cuticle punctations; (b) lateral cuticle showing pore (P)–seta (S) complex; (c) posterior tail showing lateral file of punctations (P); (d) anterior cloacal region showing position of clear patch (CP) of vas deferens opposite supplement 7; (e) spicule; (f) preloacal supplements.

Fixation-shape usually coiled. Cuticle carries transverse rows of punctations which may appear anastomosing laterally (Fig. 22a) but lateral differentiation of wider spaced rows absent. About 13 sublateral pore-seta complexes situated posterior to oesophagus region and lateral pores present in oesophagus region (Figs 20d, g, and 22b). The holotype had a small cuticle pore situated about $4\ \mu\text{m}$ posterior to amphid (Fig. 20c); not detected in other specimens. The cuticle pore located in all of the specimens about $45\ \mu\text{m}$ from anterior was accompanied by three characteristically arranged setae: two ventro-sublateral and one dorso-sublateral. R_1 sensilla not detected. R_2 sensilla $2\text{--}3\ \mu\text{m}$. R_3 sensilla $5\text{--}6\ \mu\text{m}$, located level with middle of amphid. Short dorso-sublateral subcephalic seta present. Male amphids of 4+ turns, $10.5\text{--}11.5\ \mu\text{m}$ (68–73% c.d.) wide. Female amphids of 3+ turns, $9\ \mu\text{m}$ (56–60% c.d.) wide. Buccal cavity wide with dorsal tooth and two smaller subventral teeth and anteriorly twelve rugae arranged in six pairs. Oesophagus has a $20\text{--}22\ \mu\text{m}$ posterior bulb (18–23% oesophagus length) (Fig. 21b). Tail conical, characteristically dorsally bent at tip (Fig. 20f). Lateral file of caudal punctations present (Fig. 22c) but difficult to distinguish due to curvature of the posterior section of tail and lack of lateral differentiation, from which it can be distinguished in the two species described above. Spicules $20\text{--}22\ \mu\text{m}$ long. $3\ \mu\text{m}$ precloacal spine and 7 supplements extending about $100\ \mu\text{m}$ anterior to cloaca. A clear patch in the vas deferens is located opposite the anteriormost supplement. Two opposed testes; anterior to left of gut but relative position of posterior testis difficult to determine. Female: $V = 53\text{--}54\%$. Two ovaries, opposed, reflexed: anterior to right, posterior to left.

DIFFERENTIAL DIAGNOSIS. Neotonchinae. *Neotonchus boucheri* sp. nov. can be distinguished from other members of the genus by its lack of lateral cuticle differentiation, the presence of three characteristic setae situated around the cuticle pore in the anterior oesophageal region, the paired buccal rugae and shape of the tail tip. *N. boucheri* is most similar to *N. chamberlaini* in size and spicule structure, but can be separated on the more posterior position of R_3 sensilla and position of anterior testis relative to gut.

ETYMOLOGY. The species is named after Dr G. Boucher, who first described the specimens.

REMARKS. Boucher (1976) considered these specimens conspecific with *N. chamberlaini* Wieser & Hopper, 1966, although he recognised several differences. However, examination of representatives of both material revealed evidence to support Boucher's specimens being a new species. In addition to those features mentioned in the diagnosis and Table 2, other possible characters aiding separation are the somewhat smaller dorsal tooth and the absence (?) of R_1 sensilla. The presence of transverse rows of larger punctations at every third row as depicted by Boucher (1976: Fig. 10B) could not be detected in the specimens studied here. However, the condition described by Boucher (1976) is not unknown in this group; see *Neotonchoides melotridus*.

Neotonchus meeki Warwick, 1971
(Figs 3d, 23, 24)

MATERIAL STUDIED. 2♂♂ BM(NH) 1970.245–246 and 1♀, BM(NH)1970.247: syntypes.

LOCALITY. Northumberland coast (North Sea), sublittoral very fine sand and silt.

DESCRIPTION. Body length $710\text{--}750\ \mu\text{m}$: a = 25–29; b = 6–7; c = 9; V = 49%. Cuticle has well-developed lateral differentiation of fewer rows of larger dots beginning level with the posterior oesophageal bulb (Figs 23c, 24d). Lateral cuticle pores are present but small and

difficult to detect (Fig. 23c). Posterior to the oesophageal region, the larger sublateral pores, mainly dorso-sublateral and at the edge of the area of lateral differentiation, are each associated with a seta, the pore-seta complexes (Fig. 24e): there are about 10. Male amphids have 4+ turns: the female amphid was obscured. A dorso-sublateral subcephalic seta is present (Fig. 23a). Two testes present; anterior to left of gut, posterior basically ventral to gut with perhaps a little bias to the right. Clear patch in vas deferens opposite supplements 4/5 (Fig. 24b). Tail bears a lateral longitudinal row of punctations (Fig. 3d).

REMARKS. The foregoing is based on Warwick (1971) with some additional information. Jensen (pers. comm.) found specimens of this species in the Øresund, which is the type locality of Allgen's (1935) poorly described monotypic genus *Heterocyatholaimus*. Ventral views of *N. meeki*, as Dr Jensen pointed out to me, appear identical with Allgen's drawing of the head of *H. macrolaimus*. Since there are no other characters separating the genera, at Jensen's suggestion, it is proposed that *Heterocyatholaimus* Allgen, 1935 becomes a junior synonym to *Neotonchus* Cobb, 1933. Nevertheless, Allgen's species is so badly described and based only on one female it should best be regarded as dubious. The species has also been reported from Helgoland by Lorenzen (1974).

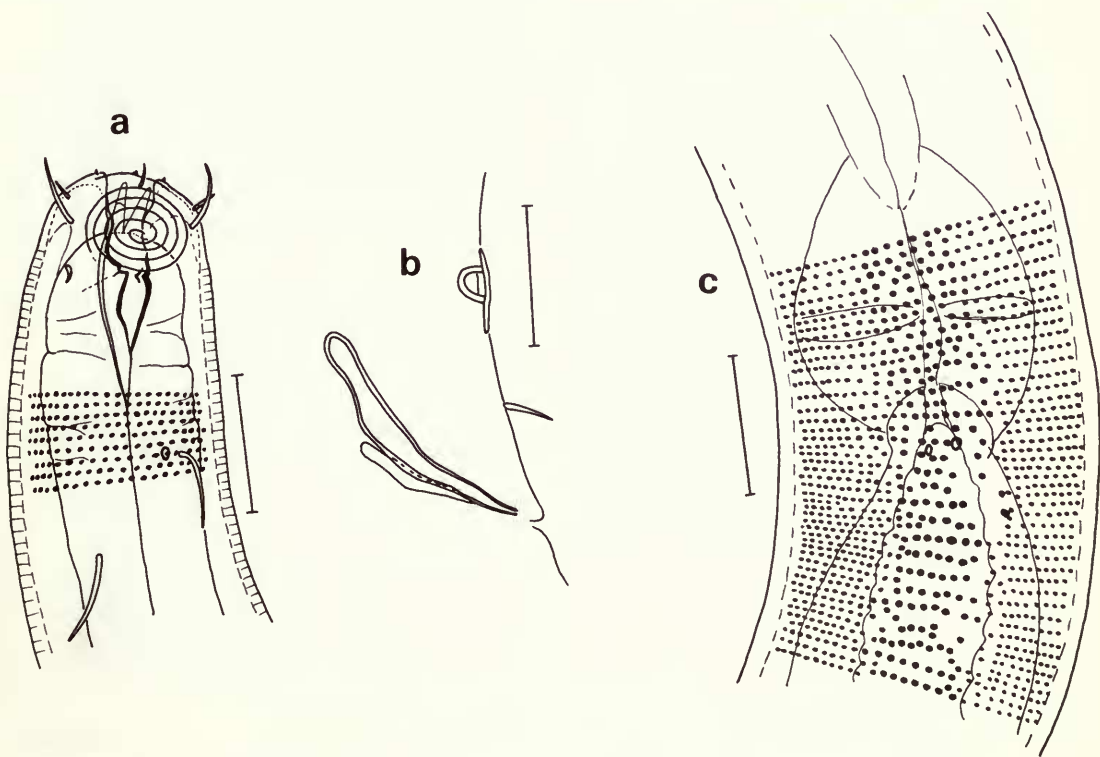


Fig. 23 *Neotonchus meeki*: (a) σ head; (b) copulatory apparatus; (c) cuticle pattern at oesophageal-intestinal junction showing beginning of lateral differentiation. Bar scales = 10 μ m.

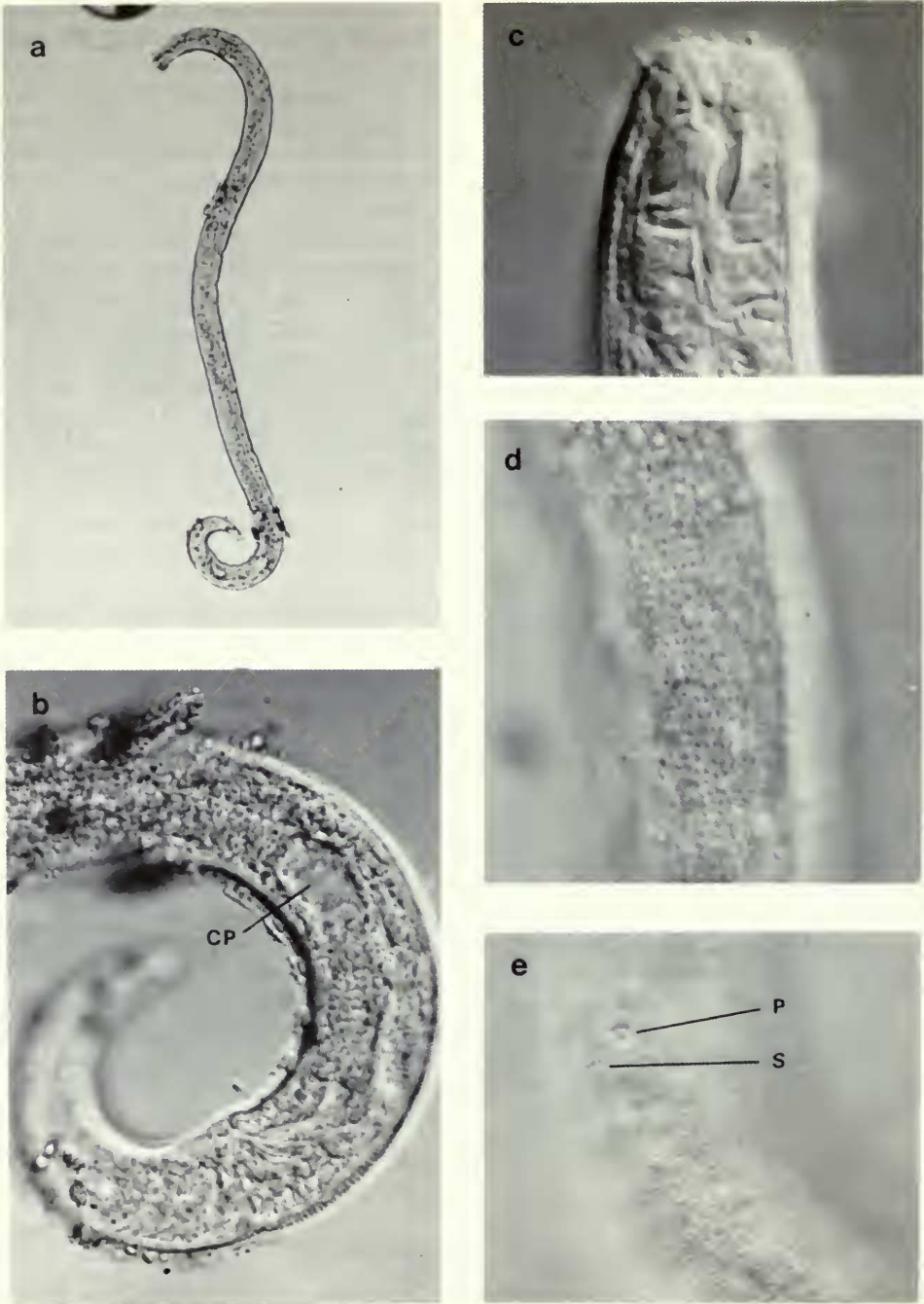


Fig. 24 *Neotonchus meeki*: (a) whole body; (b) ♂ posterior region showing position of clear patch (CP); (c) buccal cavity; (d) cuticle pattern mid-body; (e) pore (P) – seta (S) complex.

Neotonchoides melotridus (Wieser & Hopper, 1966) comb. nov.
(Figs 4a, 25a–b, 26)

Neotonchus melotridus Wieser & Hopper, 1966.

MATERIAL STUDIED. Holotype ♂, slide 119, Canadian National Collection of Nematodes.

LOCALITY. 4 miles southeast of the mouth of the North Edisto River, South Carolina, U.S.A., at a depth of 12 m.

DESCRIPTION. Body length 1140 μm ; a = 42; b = 10; c = 12 (from Wieser & Hopper, 1966). Posterior to the oesophageal region, every third transverse row tends to consist of larger, more closely spaced dots (Fig. 26e) although this is not regular: sometimes every other row is larger. In the lateral field, there is some anastomosing of the transverse rows but lateral differentiation of fewer rows is absent. Small lateral cuticle pores are present, evenly spaced throughout the body. Subventral somatic setae are present: subdorsal setae were only detected on the tail. Head diameter 12 μm . R_2 sensilla 0.7 μm . R_3 sensilla 4 μm . Dorso-sublateral subcephalic seta situated posterior to amphid (Fig. 25a). Amphid 3+ turns, 6.5 μm (55% c.d.) wide, situated between R_3 sensilla (Figs 25a, 26b). Buccal cavity well developed with prominent rugae (Fig. 26d). Spicule 25 μm , typical neotonchid shape (Fig. 26g). Feint lateral pieces detected at the distal ends of the spicule. Relatively prominent precloacal spine (Fig. 26g) and 9 precloacal supplements extending 170 μm anterior to cloaca. Prominent cuticular ridges between supplements which continue some distance anterior to last supplement. Testes opposed; anterior left, posterior right of gut. Clear patch not distinct but possibly opposite supplement 6 (Fig. 26f).

REMARKS. The R_3 sensilla appear to be slightly shorter and the amphids smaller than reported by Wieser & Hopper (1966). As Wieser & Hopper (1966) suggested, this species seems quite similar to *N. corcundus* (Gerlach, 1956) from which it can be distinguished by the more slender body (a=42 vs 28), longer spicule (25 μm vs 15.5 μm) and more posterior position of the dorso-sublateral subcephalic seta. Gerlach (1956) did not depict a precloacal spine but this was probably an oversight. There is no information for *N. corcundus* on the presence of cuticle pores, but the cuticle in the postcephalic region is depicted as having every third row larger (Fig. 4c). Decraemer & Coomans (1978) also recorded *N. melotridus* from Australia.

Neotonchoides interruptus (Warwick, 1971) comb. nov.
(Figs 4f, 25c–e, 27)

Neotonchus interruptus Warwick, 1971.

MATERIAL STUDIED. 3 ♂♂, BM(NH)1970.241–243 (syntypes).

LOCALITY. Northumberland coast (North Sea), sublittoral silt and fine sand.

DESCRIPTION. Body length 630–680 μm ; a = 30; b = 7–8; c = 10–11 (from Warwick, 1971). Cuticle lacks differentiation but in some areas there appears to be a tendency for every third row or every other row to be of larger dots. Lateral row of small cuticle pores beginning in posterior third of oesophagus and continuing to tail: most numerous in oesophageal bulb and precloacal regions (Figs 25d, e & 27f). Dorso-sublateral subcephalic seta could not be detected. Two testes; anterior left, posterior right of gut. Clear patch in vas deferens was not detected.

REMARKS. There is little to add to the description given by Warwick (1971) except for the cuticle pores and testes configuration. Warwick (1971) depicts the amphid spiralling dorsally to the centre, which is not the case. The spicule shape (Fig. 27c) clearly distinguishes this form from other known species; otherwise it seems to belong to the group characterised by small cephalic sensilla, narrow buccal cavity and small amphids.

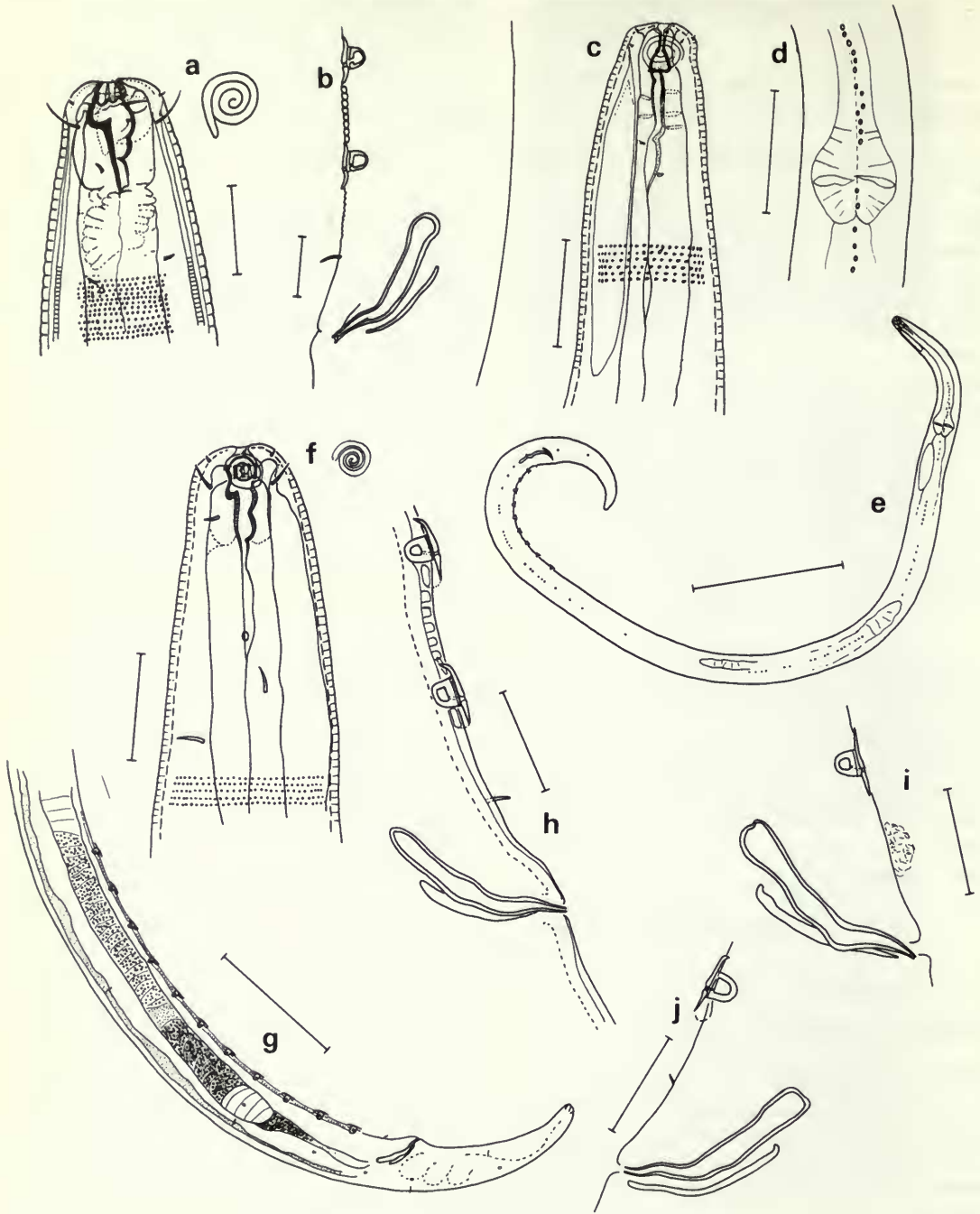


Fig. 25 *Neotonchooides melotridus*: (a) σ head, amphid shown separately; (b) cloacal region. *Neotonchooides interruptus*: (c) σ head; (d) oesophageal region; (e) whole body to show distribution of cuticle pores. *Neotonchooides warwicki*: (f) σ head, amphid shown separately; (g) posterior region; (h) σ_1 copulatory apparatus; (i) σ_3 copulatory apparatus (dirt obscuring precloacal spine); (j) σ_2 copulatory apparatus. Bar scales: e=100 μ m; g=50 μ m; others = 10 μ m.

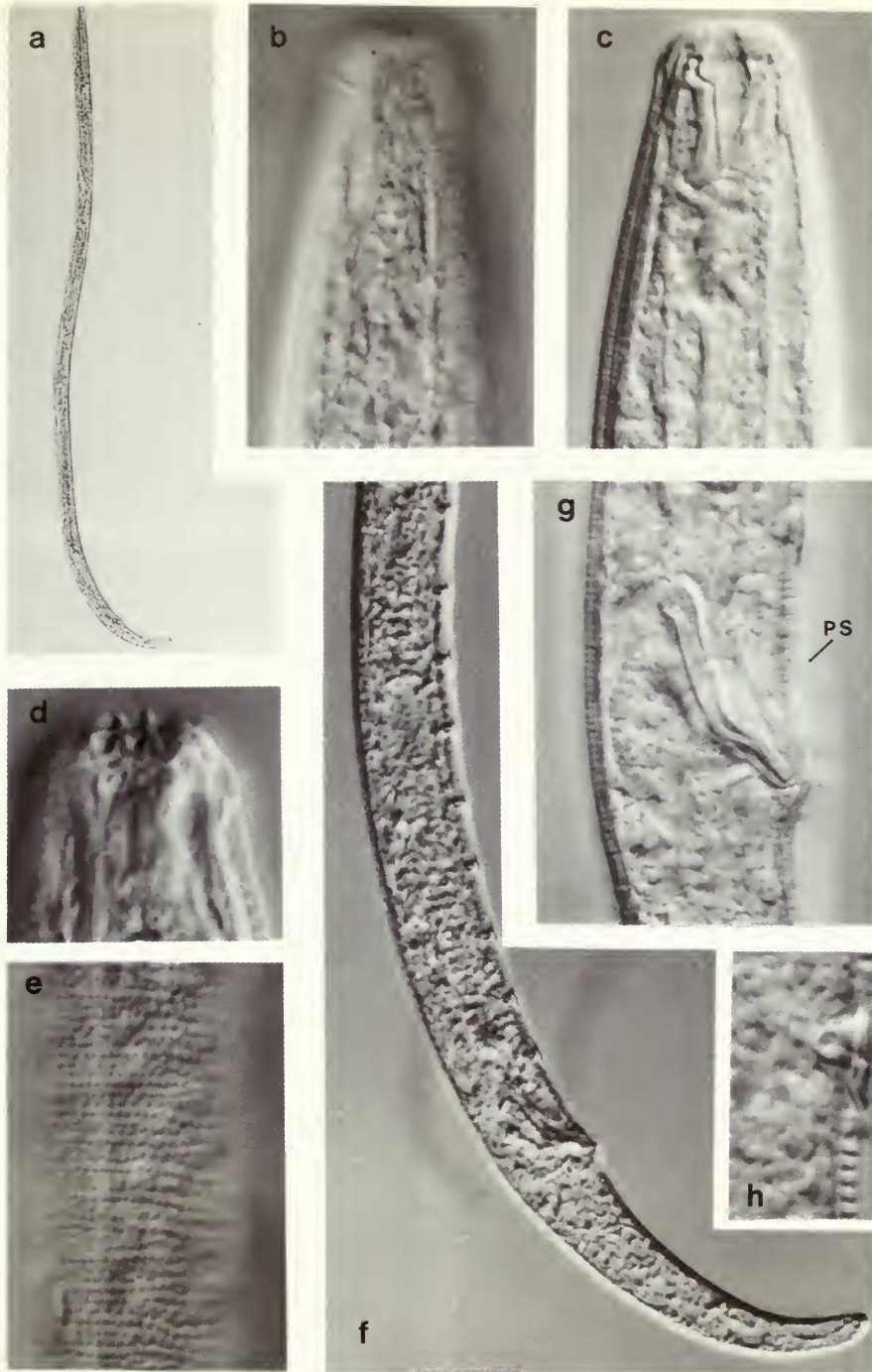


Fig. 26 *Neotonchoides melotridus*: (a) whole body; (b) anterior view showing amphid; (c) anterior view showing buccal cavity; (d) anterior view showing rugae; (e) cuticle pattern mid-body; (f) posterior region; (g) cloacal region (PS = precloacal spine); (h) detail of precloacal supplement.

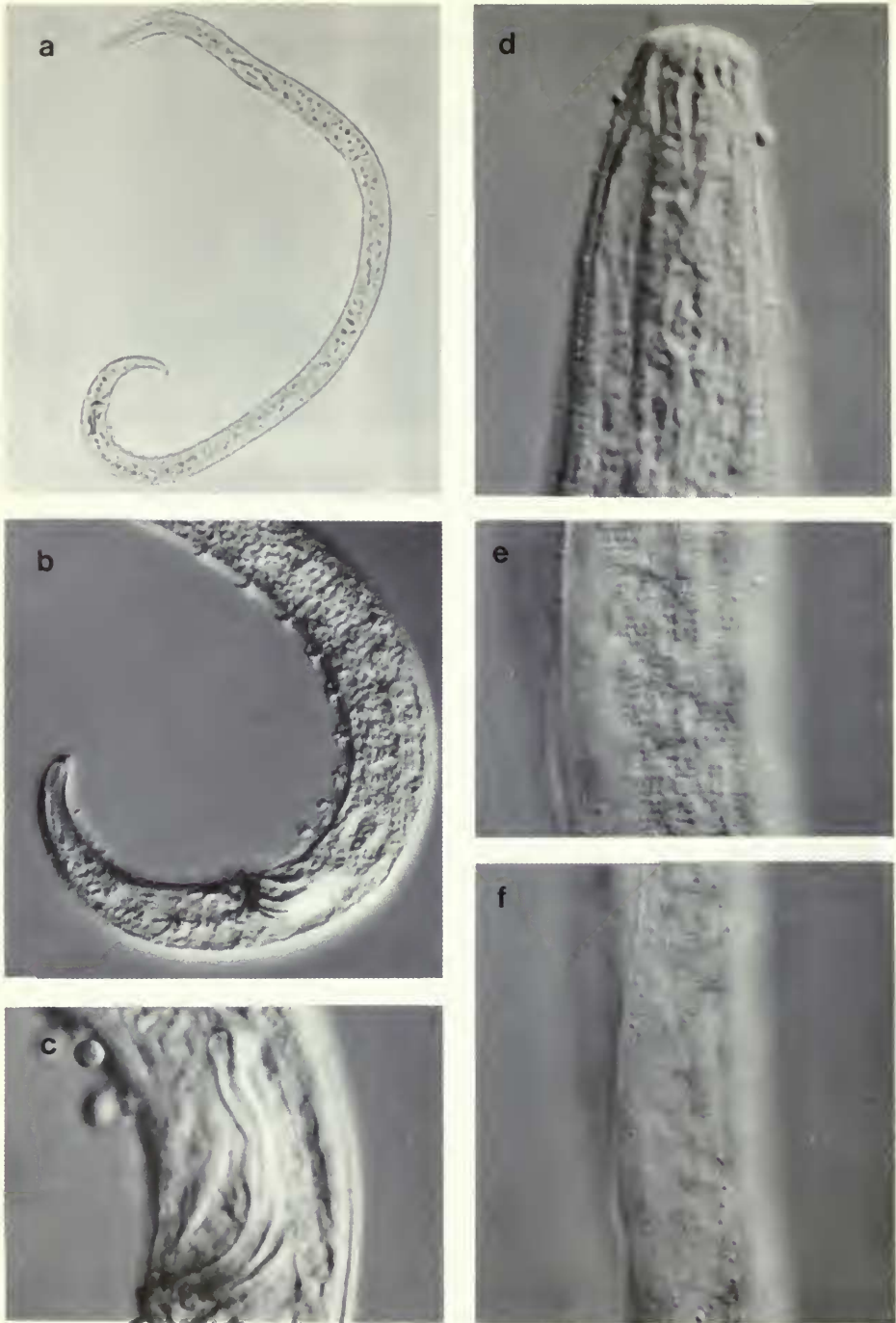


Fig. 27 *Neotonchoides interruptus*: (a) whole body; (b) posterior region showing distribution of preloacal supplements; (c) spicule; (d) anterior region showing buccal cavity; (e) lateral cuticle pattern; (f) lateral cuticle showing pores.

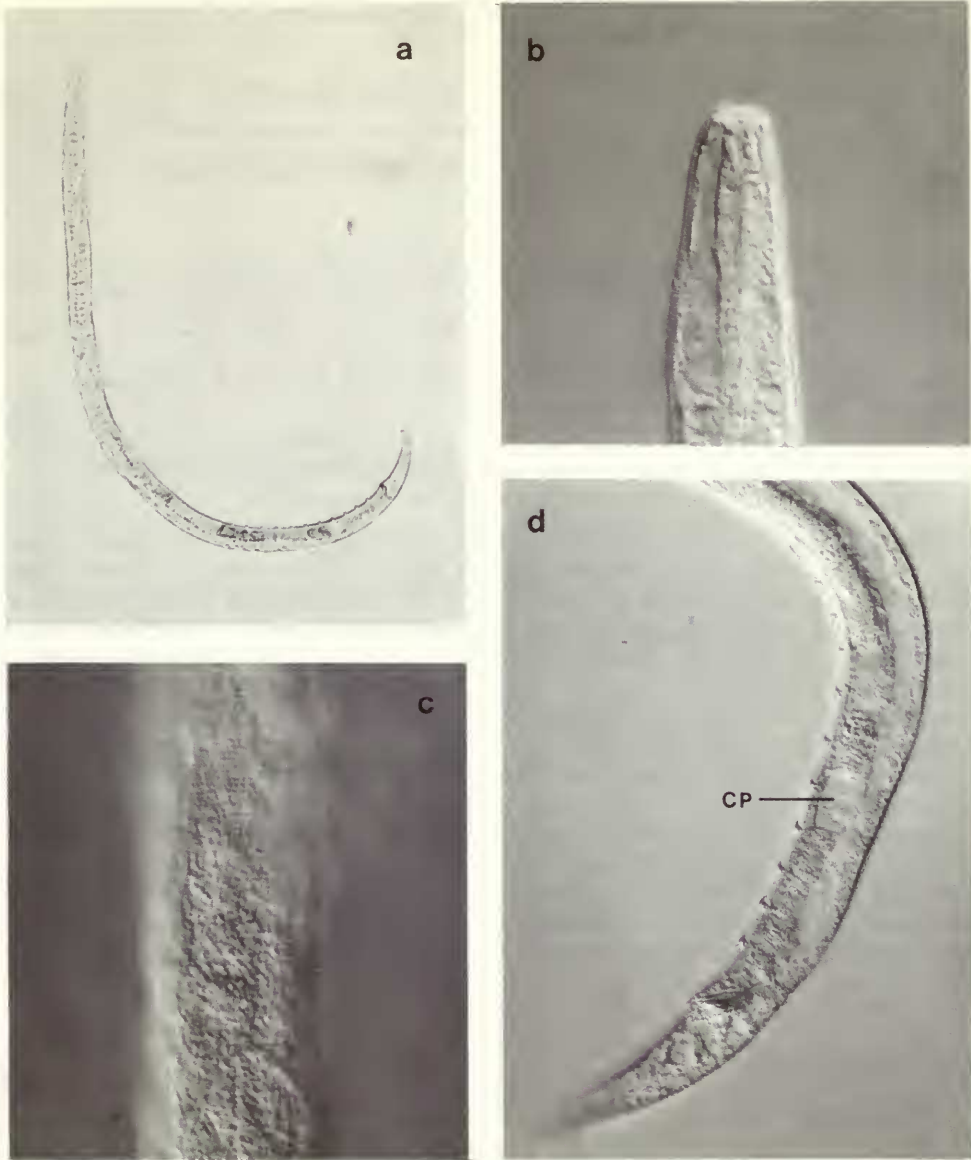


Fig. 28 *Neotonchoides warwicki*: (a) whole body; (b) anterior region showing buccal cavity and ventral excretory ampulla; (c) lateral cuticle pattern mid-body; (d) posterior region showing distribution of preloacal supplements and position of clear patch (CP).

Neotonchoides warwicki sp. nov.
(Figs 4d, 25f-j, 28)

Neotonchus corcundus sensu Warwick & Buchanan (1970) nec Gerlach, 1956.

MATERIAL STUDIED. Holotype σ_1 , paratype σ_2 , paratype σ_3 ; on slide BM(NH)1981.6.66.

LOCALITY. Northumberland coast (North Sea), sublittoral silt and fine sand.

DESCRIPTION.

Holotype σ_1 : $\frac{-}{10} \frac{102}{22} \frac{M}{24} \frac{721}{20}$ 785 μm ; a = 31; b = 8; c = 12; S = 18 μm .

Paratype σ_2 : $\frac{-}{10} \frac{95}{22} \frac{M}{24} \frac{704}{20}$ 765 μm ; a = 32; b = 8; c = 13; S = 18 μm .

Paratype σ_3 : $\frac{-}{10} \frac{102}{21} \frac{M}{23} \frac{687}{19}$ 750 μm ; a = 33; b = 7; c = 12; S = 20 μm .

Cuticle has transverse rows of small punctations: lateral dots in mid-body appear larger than medial dots (Fig. 28c) although lateral differentiation of fewer rows is absent. Very small cuticle pores are present as a lateral row, apparently evenly spaced but not easy to resolve. Few somatic setae resembling small sublateral spines. R_1 sensilla not detected. R_2 sensilla very short about 0.5 μm . R_3 sensilla 3 μm long. Short dorso-sublateral subcephalic seta present situated posterior to amphid. Male amphids 3+ turns, 3–4 μm wide, situated between R_2 and R_3 sensilla (Fig. 25f). Buccal cavity narrow, containing medium sized dorsal tooth (Figs 25f, 28b) but no ventral teeth detected. Ventral excretory ampulla prominent and opens level with amphid. Nerve ring at 60–70% oesophagus length. Oesophagus has a posterior bulb; approximately 20 μm long, 16 μm wide. Tail conical; caudal glands confined to tail. Spicules 18–20 μm long; typical neotonchid shape (Figs 25h–j). Small ventral precloacal spine. 11 precloacal supplements extending 125–165 μm anterior to cloaca. Ventral cuticle between supplements has prominent ridges. Prominent clear patch in vas deferens present level with supplement 4 in σ_1 (Fig. 25g), supplement 5 in σ_2 (Fig. 28d) but not detectable in σ_3 . Two opposed testes; anterior right, posterior left of gut in all three specimens. Females unknown.

DIFFERENTIAL DIAGNOSIS. Neotonchinae. *Neotonchoides warwicki* sp. nov. may be distinguished from other members of the genus by the small, anteriorly situated amphids. *Neotonchoides interruptus* (Warwick, 1971) also has small amphids, but they are not so far forward, the R_3 sensilla are smaller, the spicule has a different shape and the gonads are not orientated to the gut in the same way. *Neotonchoides pseudocorcundus* (Vitiello, 1971) is similar in many ways but can be separated on the position of the excretory pore, which is posterior to the nerve ring in *N. pseudocorcundus*.

ETYMOLOGY. The species is named after Dr R. M. Warwick, who had the foresight to keep a reference collection.

REMARKS. Warwick & Buchanan (1970) reported the presence of *Neotonchus corcundus* Gerlach, 1956 from off the Northumberland coast. Fortunately, the material was retained and an examination of this material revealed several important differences between it and the original description of *N. corcundus* given by Gerlach (1956): the amphid of *N. corcundus* is larger and not so anteriorly situated, the buccal cavity is much wider and more heavily cuticularised and the cephalic setae are longer. In the light of the known infraspecific variation, these differences are considered sufficient to warrant the erection of a new species.

Neotonchoides cuanensis sp. nov.

(Figs 4b, 29, 30)

MATERIAL STUDIED. 11♂♂ (Holotype ♂₅: BM(NH)1981.6.67) and 6♀♀ (Allotype ♀₂: BM(NH)1981.6.68).

LOCALITY. Intertidal sandflat, Strangford Lough, Northern Ireland (see Platt, 1977).

DESCRIPTION.

Holotype ♂ ₅ :	—	112	M	1028	1115 μm; a = 54; b = 10; c = 13; S = 19 μm
	13	18	21	18	
Allotype ♀ ₂ :	—	96	462	752	823 μm; a = 39; b = 9; c = 12; V = 56%
	13	20	21	16	

Paratypes

♂ ₁ :	L = 1100 μm; a = 58; b = 9; c = 16; S = 21 μm
♂ ₂ :	L = 1010 μm; a = 53; b = 9; c = 15; S = 20 μm
♂ ₃ :	L = 1015 μm; a = 54; b = 9; c = 14; S = 20 μm
♂ ₄ :	L = 1080 μm; a = 64; b = 9; c = 13; S = 20 μm
♂ ₆ :	L = 1015 μm; a = 54; b = 9; c = 12; S = 19 μm
♂ ₇ :	L = 1015 μm; a = 53; b = 10; c = 12; S = 20 μm
♂ ₈ :	L = 930 μm; a = 52; b = 9; c = 11; S = 20 μm
♂ ₉ :	L = 1010 μm; a = 53; b = 9; c = 13; S = 20 μm
♂ ₁₀ :	L = 915 μm; a = 48; b = 10; c = 12; S = 20 μm
♂ ₁₁ :	L = 1005 μm; a = 53; b = 10; c = 13; S = 19 μm
♀ ₁ :	L = 905 μm; a = 45; b = 8; c = 11; V = 54%
♀ ₃ :	L = 830 μm; a = 38; b = 9; c = 12; V = 56%
♀ ₄ :	L = 810 μm; a = 37; b = 9; c = 9; V = 55%
♀ ₅ :	L = 810 μm; a = 37; b = 9; c = 11; V = 59%

Cuticle bears transverse rows of fine punctations, no lateral differentiation. Transverse rows more numerous in oesophageal region of males than females (cf. Figs 29b and 29c): rows in female become more numerous posterior to oesophageal region. Very small lateral cuticle pores present throughout the body, regularly spaced but difficult to detect except in head and tail regions. Short stout sublateral somatic setae present (Fig. 29a). R₁ sensilla present as minute papillae. R₂ sensilla 1.5–2.5 μm. R₃ sensilla 4–5 μm. Dorso-sublateral subcephalic seta (?) situated posterior to level of amphid and buccal cavity. Male amphids 4+ turns, 7.5–8 μm (62–63% c.d.) wide. Female amphids 3+ turns, 6–6.5 μm (46–50% c.d.) wide. Middle of amphids situated posterior to level of R₃ cephalic setae. Head not attenuated anteriorly, giving a rather square appearance (Fig. 30c). Buccal cavity relatively wide with twelve rugae anteriorly, a pointed dorsal tooth and subventral ridges: subventral teeth could not be detected. Nerve ring 50–70 μm from the anterior, 40–60% of oesophagus length. Posterior oesophagus bulb present, 17–21 μm long, 15–20% of oesophagus length. Tail conical, 3.8–5.5 a.b.d. long with characteristic ventral bend at tail tip (Fig. 29h–m). Spicules 'L' shaped; gubernaculum a short rod lying dorsal to spicules (Figs 29e–g, 30e). Short ventral precloacal spine, 9–11 μm from cloaca. 8–10 typical precloacal supplements: in males with 10 supplements, they extended 99, 126 and 140 μm anterior to cloaca; in males with 9 supplements, they extended 81, 119, 110 and 109 μm anterior to cloaca; in males with 8 supplements, they extended 96, 86 and 98 μm anterior to cloaca. The first supplement is situated 16–23 μm (mean = 20 μm) from cloaca, so that in most specimens it lies slightly anterior to the level of the proximal end of the spicules. The cuticle is more conspicuously annulated in the areas between the supplements than elsewhere. Two testes, opposed, posterior smaller and more difficult to distinguish than the anterior; anterior left, posterior right of gut. Clear patch in vas deferens not detected. Two opposed, reflexed ovaries.

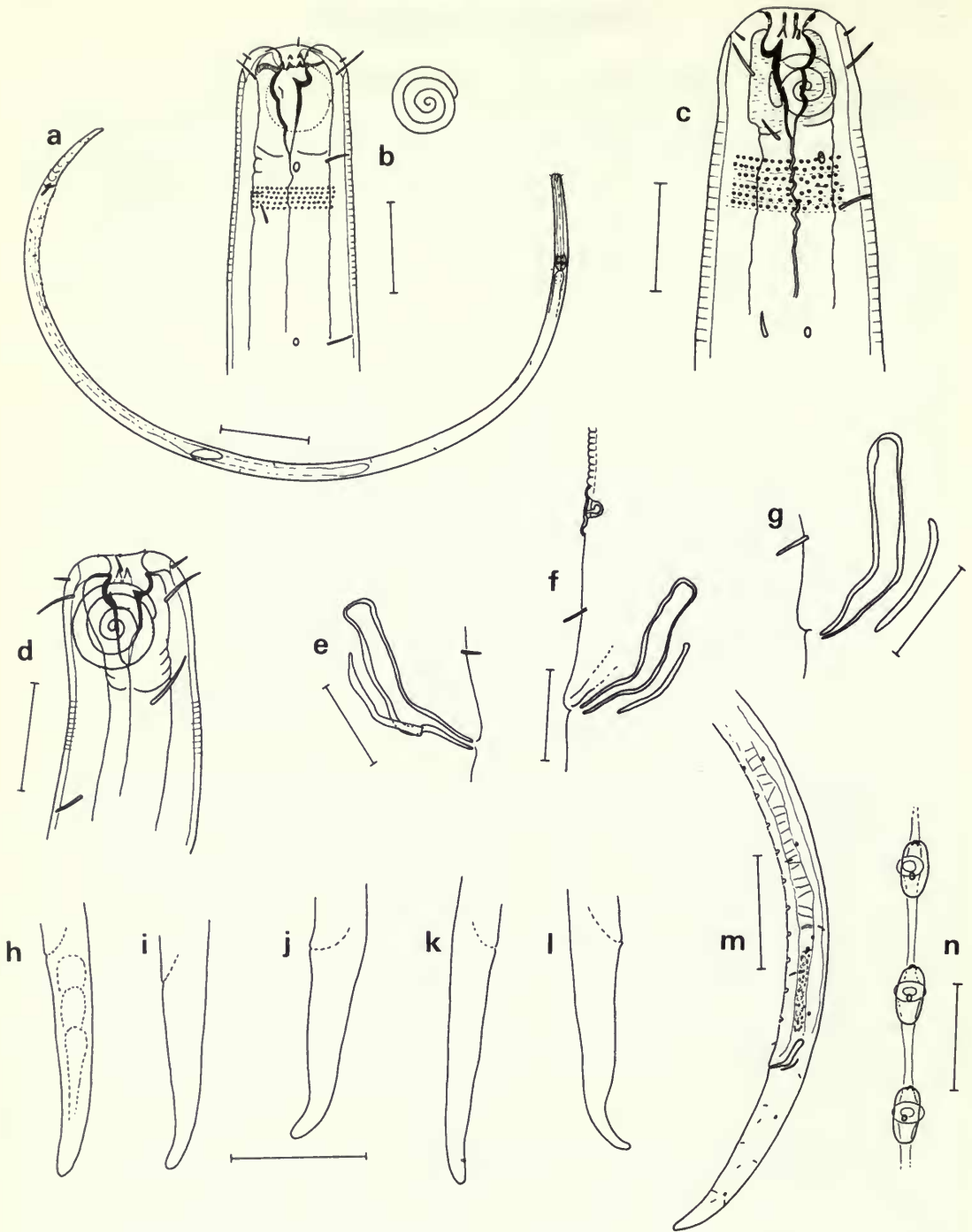


Fig. 29 *Neotonchooides cuanensis*: (a) holotype whole body; (b) holotype head; (c) allotype head; (d) σ_4 head; (e) σ_6 copulatory apparatus; (f) holotype copulatory apparatus; (g) σ_4 copulatory apparatus; (h) \varnothing tail; (i-l) tails of four different males; (m) holotype posterior region; (n) ventral view of three preloacal supplements, anterior to top. Bar scales: a = 100 μm ; h-l, m = 50 μm ; others = 10 μm .

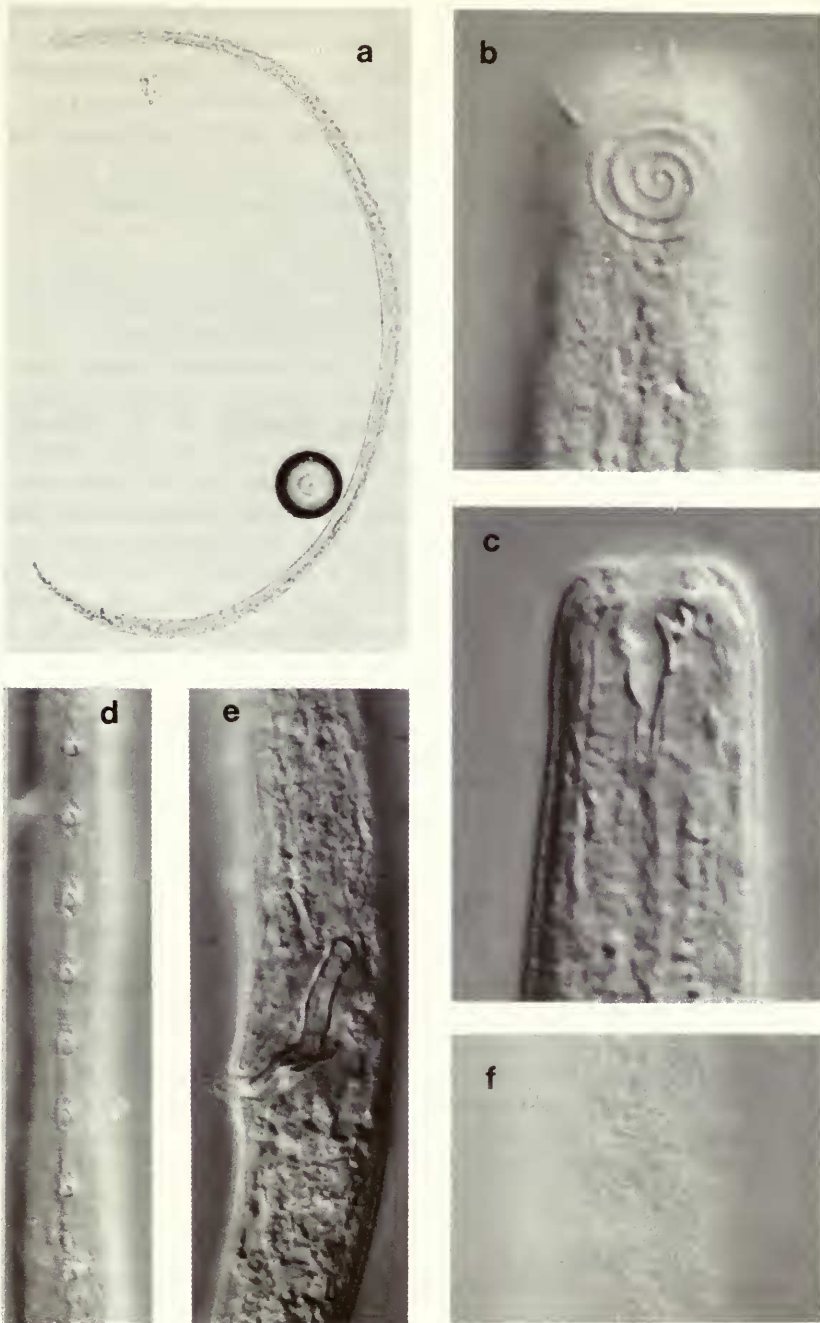


Fig. 30 *Neotonchoides cuanensis*: (a) whole body; (b) ♂ anterior region showing amphid; (c) ♂ anterior region showing buccal cavity; (d) ventral view of precloacal supplements; (e) cloacal region showing spicule shape; (f) lateral cuticle showing punctations.

DIFFERENTIAL DIAGNOSIS. Neotonchinae. *Neotonchooides cuanensis* sp. nov. most closely resembles *N. melotridus* (Wieser & Hopper, 1966) and *N. corcundus* (Gerlach, 1956) in size of R_3 sensilla, buccal cavity development, supplement number, spicule shape and tail shape. However, the males of *N. cuanensis* have larger amphids with one more turn, a different head shape, lack the cuticle pattern of larger punctations every third row and have smaller spicules and supplements.

ETYMOLOGY. The species name comes from the old Irish name for Strangford Lough: Lough Cuan.

REMARKS. The sensillum which was interpreted above as the dorso-sublateral subcephalic seta typical of the neotonchids is in a more posterior position and somewhat longer than is usual and could as easily be the first of the 'true' sublateral somatic setae; in which case the dorso-sublateral subcephalic seta would be absent or not detectable by light microscopy. In the absence of further evidence, the interpretation given in the description is preferred. *N. cuanensis* and the two species which most closely resemble it, *N. melotridus* and *N. corcundus*, were all found in shallow sediment; *N. cuanensis* from fine intertidal sand in Strangford Lough, *N. corcundus* from sand at 12 m in Kiel Bay and *N. melotridus* from 12 m depth off the North Edisto River, South Carolina, although the type of sediment was not stated. Wieser and Hopper (1966) noted that the South Carolina specimens had a 'round inflection between the proximal and distal portions of the spicules': this distinction can be seen by comparing Figs 4a and 4c. However, it is worth noting that the angularity of the spicule can also vary because of the angle from which the structure is viewed; this can be seen for *N. cuanensis* in Figs 29e-g. Wieser & Hopper (1966) also point out the difference in spicule size relative to the cloacal body diameter, but it is suspected that Gerlach's (1956) figure redrawn here as Fig 4c, may have been of a squashed specimen. *N. melotridus* and *N. corcundus* are also distinguishable on the position of the dorso-sublateral subcephalic seta. A redescription of *N. corcundus* would be useful to provide information on somatic setation, cuticle pores and gonad configuration in addition to confirming the presence of a precloacal spine.

The description of *N. cuanensis* is based on a fairly large number of individuals bearing in mind their rarity in the total nematode population. The mean length of the males, 1020 μm , was significantly greater than the mean length of the females, 836 μm , at the 0.1% level of probability. The standard deviation as a percentage of the mean, i.e. coefficient of variation, was 6.1 for males and 4.8 for females, which is within the range of infraspecific variation in body length previously reported for marine nematodes (Jensen, 1979b; Lamshead, 1982). However, a high coefficient of variation was present in the measurement 'anterior supplement to cloaca', surprisingly independent of the total number of supplements. The CV was 17%, similar to the 14% CV reported by Lamshead (1982) for the measurement 'supplement to cloaca' in *Odontophoroides paramonhystera*. This range of variation indicates that this character may be of little value in distinguishing between species.

Neotonchooides vitius (Warwick, 1971) comb. nov.
(Figs 4e, 31)

Neotonchus vitius Warwick, 1971.

MATERIAL STUDIED. 3 $\sigma\sigma$ BM(NH)1970.236-238 (syntypes).

LOCALITY. Northumberland coast (North Sea), sublittoral silt.

DESCRIPTION. Body length 690-780 μm ; a = 23-29; b = 6-7; c = 12 (from Warwick, 1971). Cuticle punctated, with lateral differentiation of fewer rows of larger dots (Fig. 31b) beginning posterior to oesophagus. The lateral cuticle pores are most numerous in oesophagus bulb region (Fig. 31c) and throughout the rest of the body are found in groups of

two, three or occasionally four (Figs 31d, e). There are small hollow lemon-shaped granules in the cells of the intestine (Fig. 4e). Two testes, opposed; anterior left, posterior right of gut. Clear patch in vas deferens situated opposite supplement 5 (Fig. 31f).

REMARKS. As pointed out by Warwick (1971), what he refers to as lateral punctations are indeed the cuticle pores. However, they could not be resolved into paired structures as depicted by Warwick (1971). *N. vitius* can be distinguished from other species in the genus by the presence of groups of pores, the lateral differentiation and the ventral kink in the dorsal surface of the spicule (Fig. 31g). The only other reference to lemon-shaped granules in the intestine wall appears to be that of Cobb (1920) in his description of *Nannolaimus guttatus*, where he describes them as 'hollow shells, more or less thick-walled'.

Nannolaimus fusus Gerlach, 1956
(Fig. 5a, 32)

MATERIAL STUDIED. 1♂, BM(NH)1981.6.69.

LOCATION. South Bay, Co. Down, Northern Ireland (Boaden & Platt, 1971).

DESCRIPTION.

♂: $\frac{-}{12} \frac{140}{17} \frac{M}{19} \frac{1132}{18}$ 1245 μm ; a = 66; b = 9; c = 11; S = 26 μm

Body relatively elongated (Fig. 32a). Cuticle has transverse rows of small punctations but lateral differentiation absent. Lateral file of cuticle pores present, about 30 μm apart. Sparse somatic setae. R_1 sensilla setose, 3.5 μm long. R_2 sensilla 11 μm . R_3 sensilla 6 μm , situated only very slightly posterior to R_2 sensilla. Dorso-sublateral subcephalic seta not detected at mid-amphid level and the long seta situated level with the posterior margin of the amphid is probably the first of the sublateral somatic setae. Amphid large, 6+ turns and longitudinally elongated; 18 μm long and 11 μm (85% c.d.) wide. Oesophagus widens posteriorly to a bulb but the latter not easy to detect. Tail cylindrical with rounded tip; 6 a.b.d. long. Spicules relatively long, 1.4 a.b.d., with a central division. Gubernaculum lies parallel to spicules. Small ventral precloacal spine and two subventral postcloacal spines (Fig. 32e). 10 typical precloacal supplements, extending 218 μm anterior to cloaca: first supplement 33 μm from cloaca and remainder about 20 μm apart. Two opposed testes; anterior left, posterior probably right of gut but difficult to be certain. No clear patch observed in vas deferens.

REMARKS. There are two apparent differences between the specimen from South Bay and the only other description, that of Gerlach (1956). Gerlach (1956) found alternating rows of large and small dots whereas this could not be detected here. However, Gerlach depicted this from a medial view whereas the Irish specimen was laterally orientated. Since it was decided not to risk damaging the only specimen by rolling it to observe a medial view, this difficulty will have to remain unresolved. The spicule was similar in general outline shape but Gerlach (1956) did not depict a central division and drew the gubernaculum strongly, lying lateral to the distal end of the spicule. Since both Gerlach's interpretation and that given here differ from the usual neotonchid spicule and gubernaculum, it seems preferable to await further evidence before using this difference to create a separation. Gerlach (1956) quotes the length of the spicule as 20 μm , but if his measurement of the cloacal diameter is correct (25 μm), the spicule is also about this length. In most other respects, the specimen from South Bay conforms well with Gerlach's description, especially in terms of body size and shape, setose R_1 sensilla, relative lengths of R_2 and R_3 sensilla, amphid size and number of turns and supplement number (9 vs. 10).

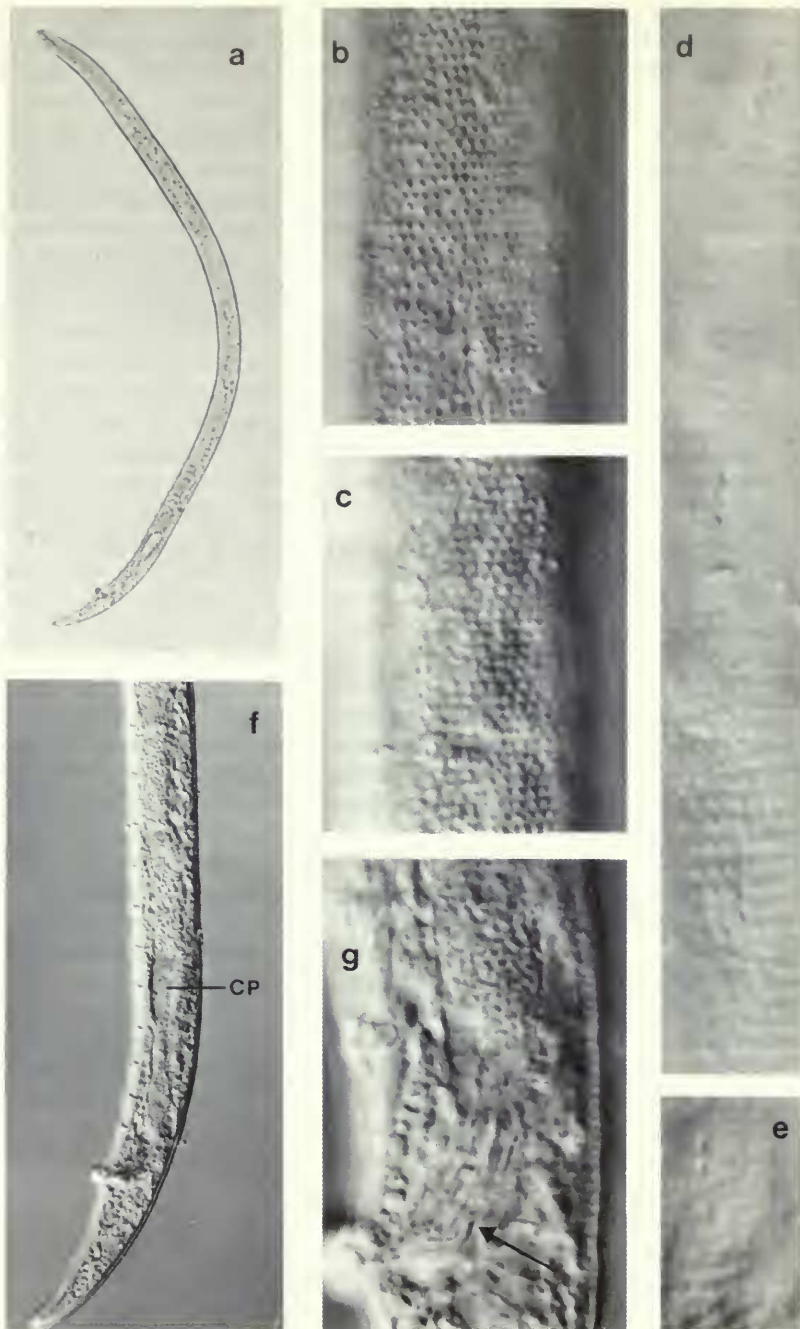


Fig. 31 *Neotonchooides vitius*: (a) whole body; (b) lateral cuticle pattern mid-body; (c) lateral cuticle showing pores level with oesophagus bulb; (d) cuticle pores mid-body; (e) group of four cuticle pores from cloacal region; (f) posterior region showing supplements and clear patch (CP); (g) cloacal region, arrow showing position of kink in spicule.

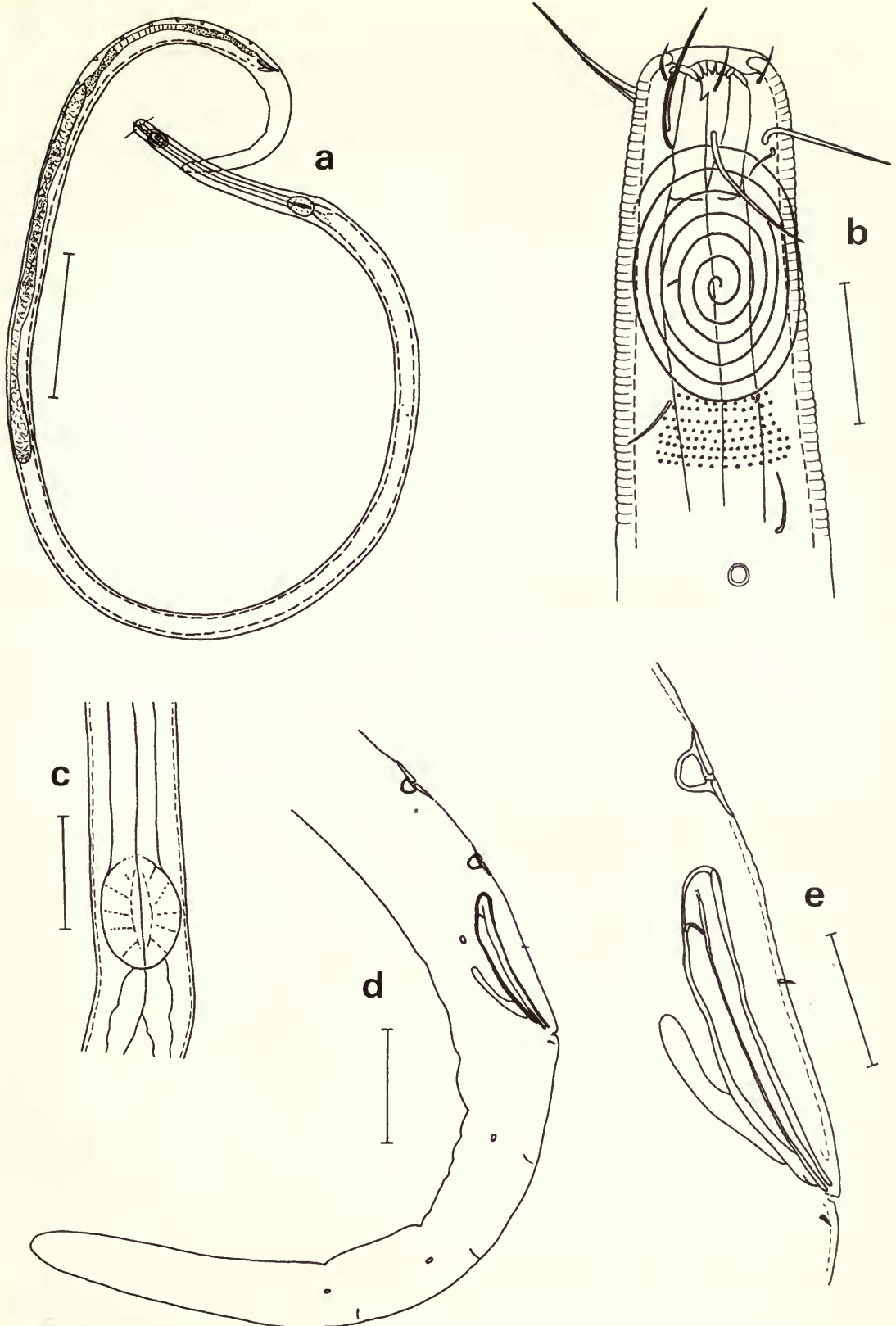


Fig. 32 *Nannolaimus fusus*: (a) ♂ whole body; (b) ♂ head; (c) posterior oesophageal region; (d) ♂ posterior region; (e) copulatory apparatus. Bar scales: a = 100 μm ; c, d = 20 μm ; b, e = 10 μm .

Nannolaimus phaleratus (Wieser & Hopper, 1966) comb. nov.
(Figs 5b, 33a–c, 34)

Neotonchus phaleratus Wieser & Hopper, 1966

MATERIAL STUDIED. Holotype ♂, slide 120, Canadian National Collection of Nematodes.

LOCALITY. 4 miles southeast of the mouth of the North Edisto River, South Carolina, U.S.A., at a depth of 12 m.

DESCRIPTION. Body length = 970 μm . Maximum body diameter 19 μm ($a = 51$). Cuticle has transverse rows of punctations; no lateral differentiation. The punctations are less pronounced and smaller posterior to the oesophagus with a clear discontinuity in annule width level with the posterior of the oesophagus. In mid-oesophagus, there are 14 rows of dots per 10 μm whilst in the mid-body area, there are 19–20 rows per 10 μm . Cuticle pores could not be detected. Apart from setae situated laterally just posterior to the amphid and on the tail, somatic setae were also not detected. R_1 sensilla setiform, 2 μm long. R_2 sensilla 8 μm . R_3 sensilla 12 μm . Dorso-sublateral subcephalic seta present level with the amphid centre. Amphid 4+ turns, longitudinally elongate. Buccal cavity with rugae anteriorly, a short vestibule and then narrow with a small dorsal tooth-like projection at the entrance to the narrow section (Figs 33b, 34b). Oesophagus 116 μm long ($b = 8$) with a 19 μm long posterior bulb (16% of total oesophagus length). Tail 96 μm long ($c = 10$). 8 preloocal supplements. Two testes, both situated left of gut and apparently lying in tandem, although it is difficult to be sure. There appears to be a clear patch in the vas deferens situated opposite supplement 6.

REMARKS. The specimen studied conformed well with the description given by Wieser & Hopper (1966), based on two males and one female, although the holotype appeared to be somewhat narrower than reported by them. According to Wieser & Hopper (1966), the female amphids are smaller and only 3+ turns. Wieser & Hopper (1966) considered that this species most closely resembled *Neotonchus chamberlaini*, having similar shaped spicules. However, there are sufficient differences at the generic level as discussed earlier which suggest that *N. phaleratus* should be placed in a different genus together with *Nannolaimus fusus*, the two being easily distinguished by the relative lengths of the R_2 and R_3 sensilla.

Filitonchus filiformis (Warwick, 1971) comb. nov.
(Figs 5c, 33d–e, 35)

Neotonchus filiformis Warwick, 1971

MATERIAL STUDIED. 3 ♂♂, BM(NH)1970.233–235 (syntypes).

LOCALITY. Northumberland coast (North Sea), sublittoral silt.

DESCRIPTION. Body length 1190–1300 μm ; $a = 86$ –99; $b = 12$; $c = 16$, $S = 15$ –16 μm (from Warwick, 1971). Cuticle with transverse rows of small punctations; no lateral differentiation. Minute cuticle pores can be detected; difficult to distinguish any pattern and appear to be few in number. R_1 sensilla not detected; R_2 and R_3 sensilla setose. Dorso-sublateral subcephalic seta present level with the posterior part of the amphid (Fig. 33d). Long sublateral cervical setae present (Figs 33d & 35b) but somatic setae otherwise sparse. Amphids 4+ turns. Two opposed testes; anterior right, posterior left of gut. An obvious clear patch in the vas deferens is present level with supplements 4 and 5 (Fig. 35c).

REMARKS. The foregoing conforms well with the original description by Warwick (1971). The sharp pointed dorsal tooth described by Warwick (1971) could not be detected but the specimens were not in good condition at the anterior.

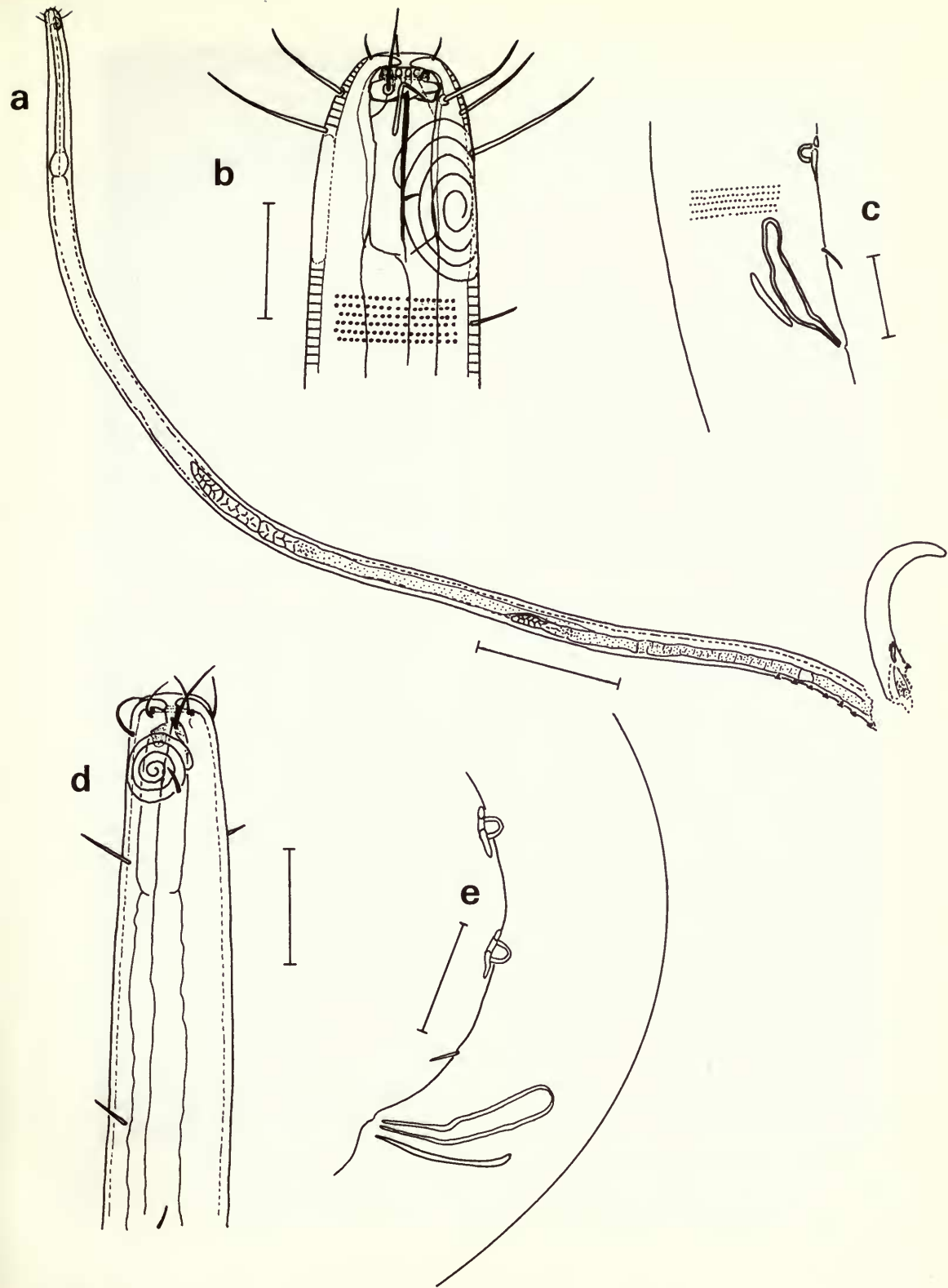


Fig. 33 *Nannolaimus phaleratus*: (a) holotype whole body; (b) holotype head; (c) holotype cloacal region. *Filitonchus filiformis*: (d) σ_1 anterior region; (e) σ_1 cloacal region. Bar scales: a = 100 μm ; others = 10 μm .

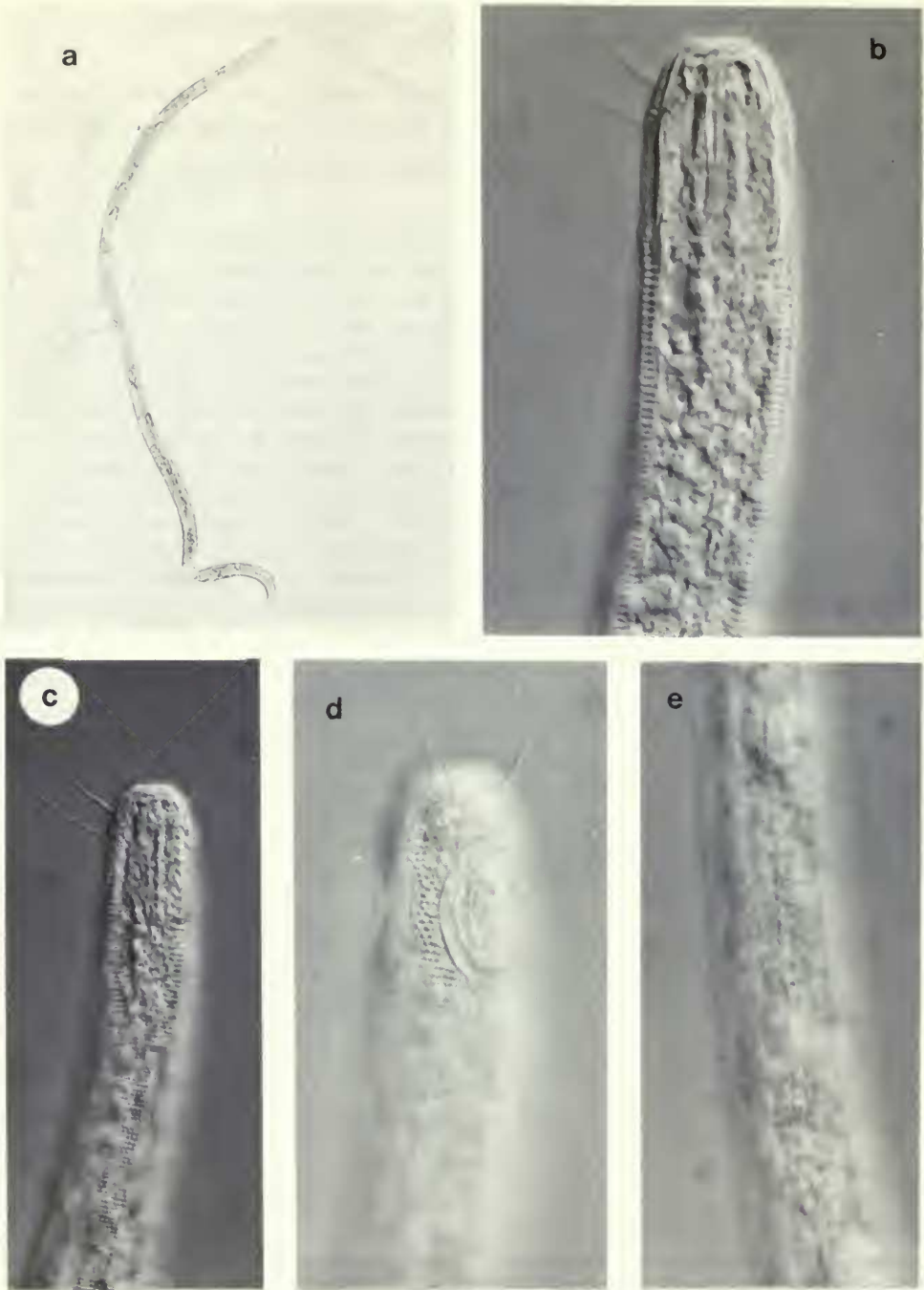


Fig. 34 *Nannolaimus phaleratus*: (a) whole body; (b) anterior region showing R₁ sensilla and buccal cavity; (c) anterior region showing cephalic sensilla and cuticle punctations; (d) anterior region showing amphid and cephalic punctations; (e) lateral cuticle punctations mid-body.

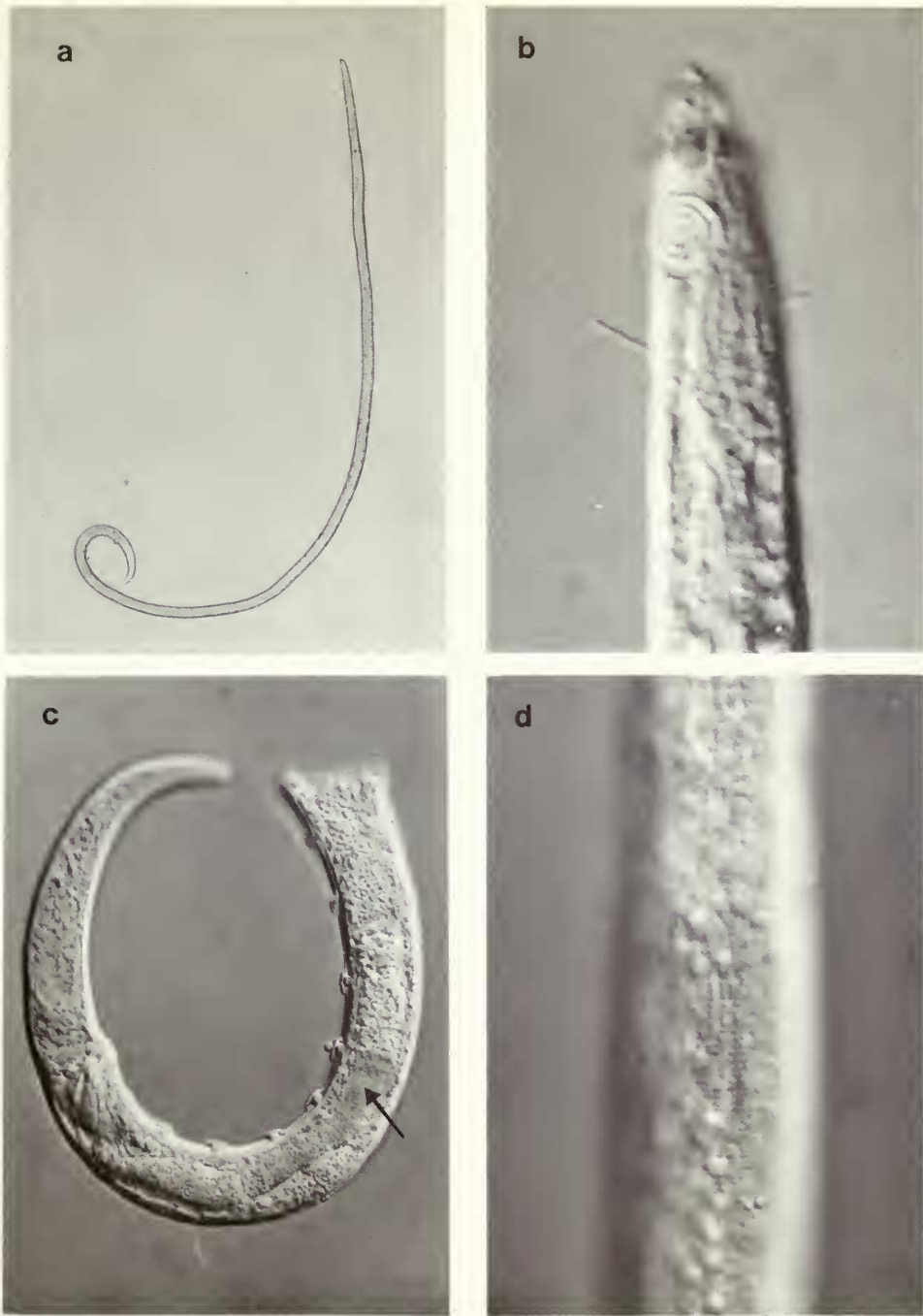


Fig. 35 *Filitonchus filiformis*: (a) whole body; (b) anterior region showing amphid; (c) posterior region showing supplements and clear patch (arrowed); (d) lateral cuticle markings.

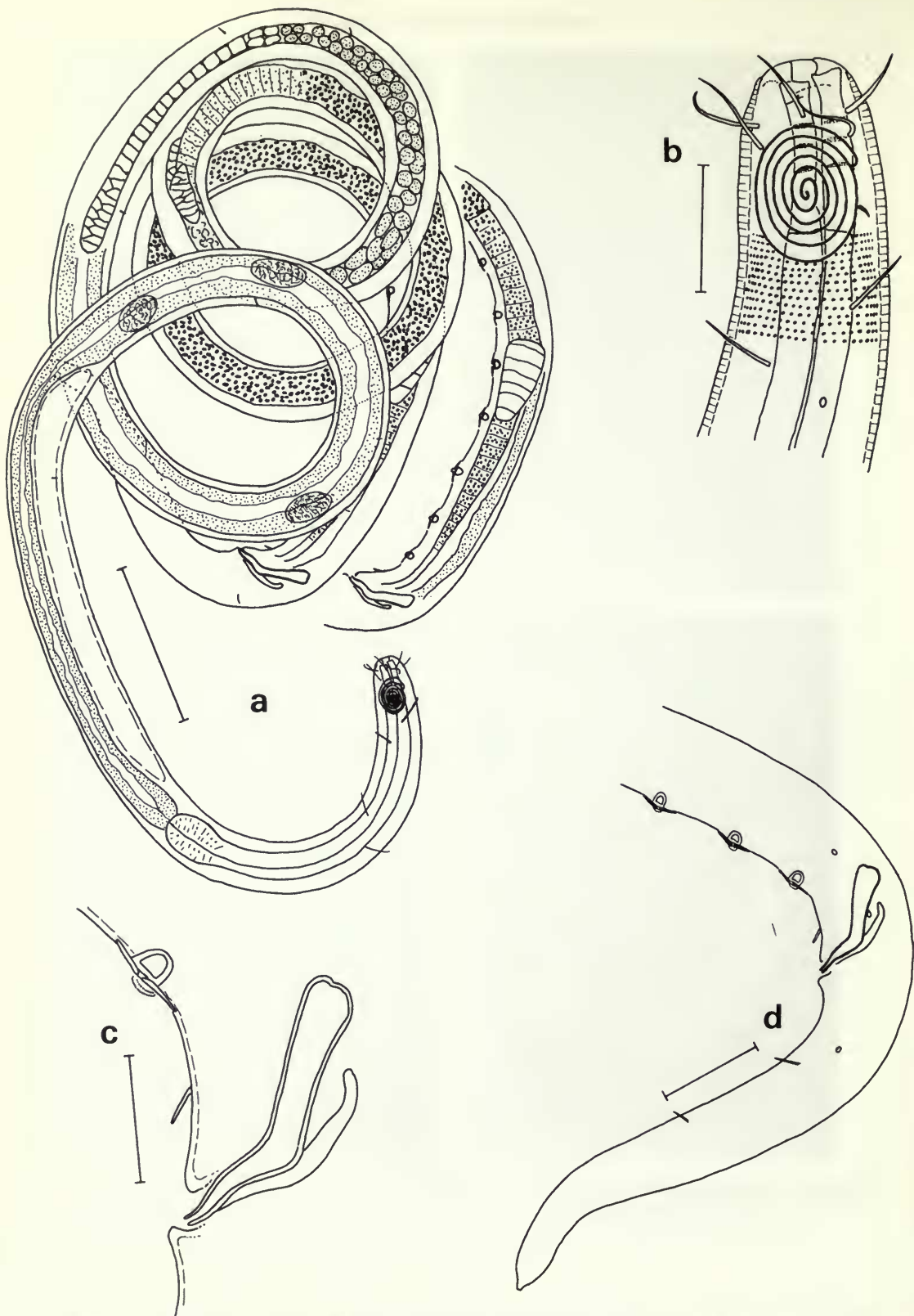


Fig. 36 *Filitonchus ewensis*: (a) whole body; (b) head; (c) copulatory apparatus; (d) posterior region. Bar scales: a = 50 μm ; d = 20 μm ; b, c = 10 μm .

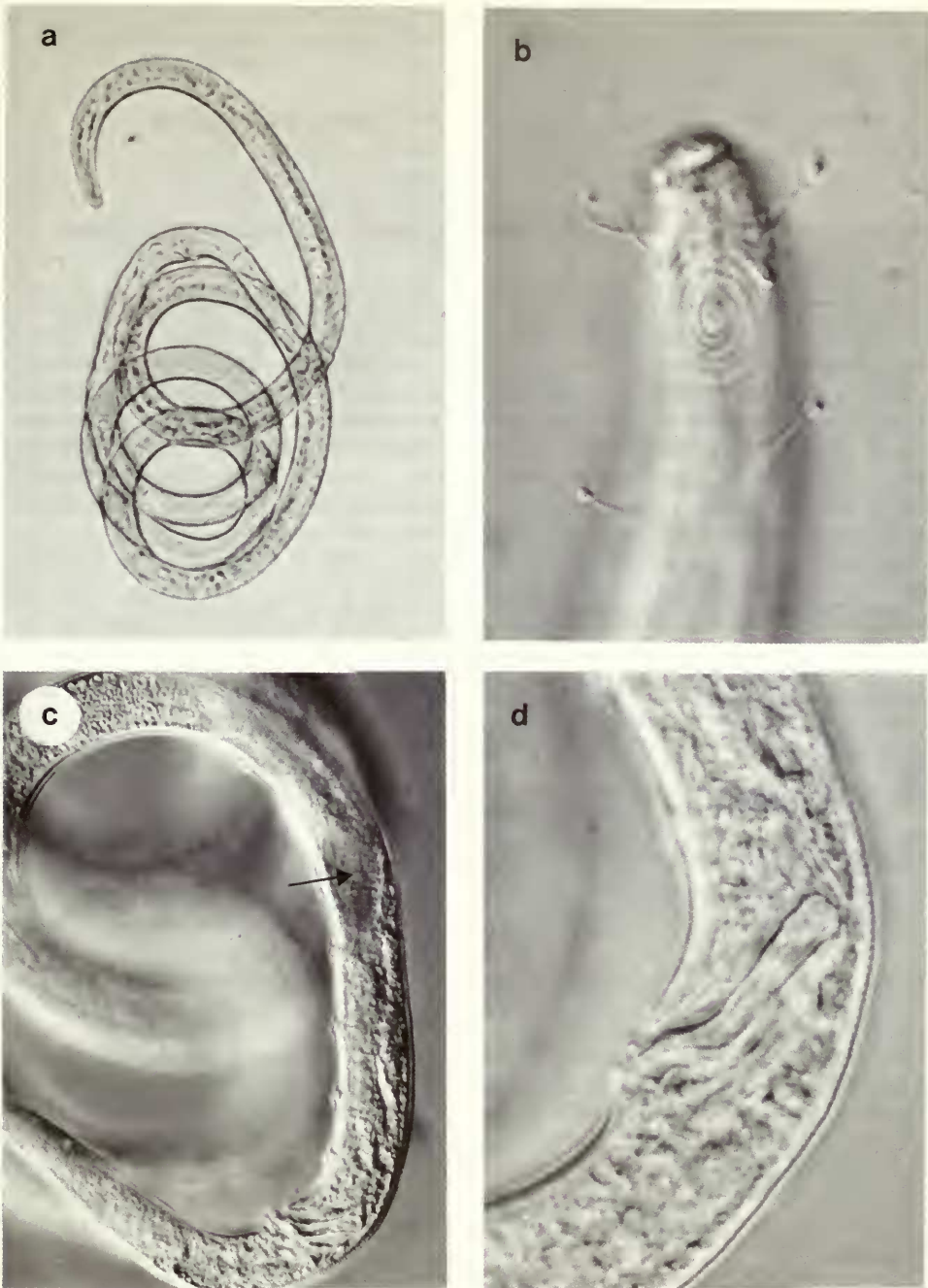


Fig. 37 *Filtonchus ewensis*: (a) whole body; (b) anterior region showing amphid and cervical setae; (c) posterior region showing clear patch (arrowed); (d) cloacal region showing spicule shape.

Filitonchus ewensis sp. nov.
(Figs 5d, 36, 37)

MATERIAL STUDIED. Holotype ♂: BM(NH)1981.6.70.

LOCALITY. Intertidal sand, Firemore Bay, Loch Ewe, Wester Ross, Scotland.

DESCRIPTION.

Holotype ♂: $\frac{-}{10} \frac{103}{17} \frac{M}{17} \frac{1275}{18}$ 1370 μm ; a = 81; b = 13; c = 14; S = 23 μm

Cuticle bears transverse rows of punctations; no lateral differentiation. Small cuticle pores present as a lateral file throughout the body. Long cervical setae present on the anterior half of the oesophageal region which are bilaterally symmetrical. Sparse short somatic setae present on the rest of the body. R₁ sensilla not detected. R₂ sensilla 6 μm . R₃ sensilla 8 μm , situated slightly posterior to R₂ sensilla. Short dorso-sublateral subcephalic seta present level with middle of amphid. Amphids large, 6+ turns and longitudinally oval; 11 μm long and 8 μm (70% c.d.) wide. Buccal cavity narrow with no sign of a cuticularised dorsal tooth. Oesophagus ends in a 17 μm long bulb (17% of total oesophagus length). Long renette cell situated posterior to oesophagus (Fig. 36a). Tail gently tapering; 5 a.b.d. long. Spicules typical neotonchid shape and broad proximally (Fig. 37d). Precloacal spine situated 9 μm anteriorly. 7 typical precloacal supplements extending 115 μm from cloaca. Two opposed testes; anterior right, posterior left of gut. A prominent clear patch is situated between supplements 4 and 6 (Figs 36a & 37c).

DIFFERENTIAL DIAGNOSIS: Neotonchinae. *Filitonchus ewensis* sp. nov. may be distinguished from the other species in the genus by the larger amphid with a greater number of turns and shape of the spicules.

ETYMOLOGY. The species name comes from the type locality; Loch Ewe.

REMARKS. Despite only one specimen being available, it seems well enough characterised to warrant the erection of a separate species. However, the condition of the buccal cavity was not very good and needs further investigation when more specimens become available. The presence of a long renette cell was also found in *Nannolaimus guttatus* by Cobb, 1920.

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